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Bionomics and Zoogeography of Tiger Beetles of Saline Habitats in the Central United States (Coleoptera: Cicindelidae)[1]

By

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INTRODUCTION

Cicindelids of saline habitats first came to my attention when, upon visiting a salt flat in Stafford County, Kansas, for the first time, in October 1961, I was amazed to find a species of tiger beetle *(Cicindela togata)* abundant on the barren, salt-encrusted soil. Further collecting in such habitats revealed that there are a number of species adapted for living in saline areas that are found nowhere else. It seemed worthwhile to investigate how these insects "make a living" in such harsh environments and how they came to be distributed and adapted to saline habitats scattered widely over the central United States.

A survey of the literature showed that although adults of North American cicindelids are quite well known taxonomically, relatively little work has been done on the life history, ecology, or zoogeography of most species. Shelford (1907, 1908, 1911, 1913d, 1917) and Criddle (1907, 1910) have done excellent work on the life cycles and ecology of a number of species in northeastern North America. Hamilton (1925) described the larvae of about 25 United States species and Spangler (1955) described another. Many other authors have made some mention of bionomics in addition to other subjects; Ortenburger and Bird (1933) are among the few to mention cicindelids of saline habitats in the central United States. Several general works with zoogeographical emphasis have included some or all cicindelids of the United

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States (Horn, 1908-1915; Papp, 1952; Schilder, 1953b; Rivalier, 1950, 1954, 1957, 1961, 1963). Studies by Wickham (1904a, b), Cazier (1948, 1954), and Rumpp (1956, 1957, 1961), have included species of saline habitats of the southwestern United States and Mexico, a few of which also occur in the central United States. Except for brief habitat and distribution notes in many papers, these are the only works having any direct connection with the species in this study. Many of the minor works and others dealing with foreign species will be mentioned later.

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MATERIALS AND METHODS

As many saline habitats as possible in the central United States (southern Nebraska, Kansas, western Missouri, and Oklahoma) were visited during 1963-1965 to obtain specimens and data. Many were visited repeatedly to obtain information on seasonal distribution. When possible, large series of specimens were collected for statistical analysis. Both larvae and adults were collected alive and brought into the laboratory for life history studies.

In the laboratory, larvae were kept in tall jars full of soil from their natural habitat and were fed either small arthropods from weed sweepings or Mediterranean flour moths, *Anagasta kuehniella*, from a stock culture. Adults and young larvae resulting from their oviposition were kept in terraria partly filled with soil from saline habitats. A small Stender dish with water and a shelter made from a card with its corners bent down were provided, and the adults were given food similar to that offered the larvae. The temperature of the laboratory was a nearly constant 24.5°C, although occasionally a gooseneck lamp was placed over the terraria to provide more heat. The soil of the larval and adult containers was moistened occasionally. Eggs, pupae, and teneral adults were kept in Stender dishes for observation.

In addition to over 3600 specimens collected personally, over 15,400 specimens were borrowed from or examined at most of the major insect collections in the United States and Canada. More details about certain methods will be given later.

SALINE HABITATS

Saline terrestrial habitats are found throughout much of the world. The most widely distributed are coastal, including beaches, tidal flats, and salt marshes. Chapman (1960) has reviewed the extensive literature on coastal saline habitats. Coastal salt marshes are generally densely vegetated and thus unfit for cicindelids; however, tidal flats and beaches are often well populated.

Away from the coast, one may encounter inland saline habitats, which are not subjected to periodic inundation by tides or wave action. Inland saline and alkaline habitats are found in all continents, primarily in semiarid and arid regions. These inland areas are associated with three types of soil; one contains underground deposits of sodium chloride, another has excess sodium chloride and sodium sulfate in the surface layers, and the third has sodium sulfate, sodium carbonate, and/or magnesium sulfate in a subsurface layer. The soils with subsurface deposits are called alkali soils (Chapman, 1960). Richards (1954) defines a saline soil as one that contains an excess of soluble salts (the electrical conductance of a saturated paste in the unit of measure; the arbitrary value of 4 mmhos/cm is the lower limit of saline soils) and an alkali soil as having an excess of exchangeable sodium (15% exchangeable sodium is the lower limit of alkali soils). Soils with an excess of both soluble salts and exchangeable sodium are called saline-alkali soils. The pH of saline soils is ordinarily less than 8.5; that of alkali soils is above 8.5, sometimes reaching 10. The pH of saline-alkali soils is variable, but usually below 8.5 (Richards, 1954). The commonness of saline and alkaline habitats in arid and semiarid regions is due partly to the evaporation rate and low rainfall of such areas, which decrease the leaching of salts into the ground water where they can be carried away. Restricted drainage is another factor contributing to the salinization of soils; temporary or permanent flooding, as well as irrigation, may raise the ground water level and cause accumulation of salts at the surface (Richards, 1954). Alkalization of soil occurs by cation adsorption on the surfaces of soil particles as a consequence of electrical charges (Richards, 1954).

The original source of the salts is the minerals which weather out of the rocks of the earth's crust; however, a more direct source is from marine deposits of earlier geologic ages. The salts are usually moved by surface and ground water to areas in which they are concentrated.

Most saline habitats contain characteristic vegetation which has been variously classified. Chapman (1960) used the terms halophyte and glycophyte (mesophyte or non-halophyte), but said that one cannot always readily distinguish between them. Many halophytes exhibit characteristic physical modifications, such as a glaucous appearance, succulence, water storage hairs, small leaves, a glabrous surface, and salt-secreting glands (Chapman, 1960).

The vegetation of coastal and inland saline habitats is often very similar, often consisting of closely related species; however, there are greater differences from one continent to another. Both coastal and inland saline habitats often exhibit a zonation of vegetation, primarily in response to varying degrees of salinity, although other factors such as drainage and topography are important. Chapman (1960) reviewed many studies of this phenomenon. In coastal areas, a definite succession to mesic conditions has been found; however, Chapman (1960) said that in inland areas, the zonation is usually static and the vegetation must be considered an edaphic climax. Baalman (1965), in a study of a salt flat in Oklahoma, decided that little change in vegetation could be expected in highly saline areas. Ungar (1965) called the vegetation of a Kansas salt marsh a sub-climax which would change to a mesic climax if excess salts and water were removed.

Fewer studies have been made on the fauna of saline habitats. Davis (1962) surveyed the seasonal abundance of insects in North Carolina coastal salt marshes. Smalley (1960) studied the energy flow in populations of a Georgia salt marsh grasshopper, and Teal (1962) reported on energy flow in an entire Georgia salt marsh ecosystem. Ortenburger and Bird (1933), Jackson and Warfel (1933), and Williams (1954, in Baalman, 1965) studied the ecology of several Oklahoma salt flats. Lengerken (1929) did a detailed study of halophilic beetles of the coast of Germany. Pearse, Humm and Wharton (1942) studied the ecology of sand beaches in North Carolina.

The area here arbitrarily called the central United States (southern Nebraska, Kansas, western Missouri, and Oklahoma) has been variously subdivided by biologists and geographers. The system given in Kendall, Glendinning, and MacFadden (1958) seems adequate: the western three-fourths of Nebraska, the western two-thirds of Kansas, and the Oklahoma panhandle are in the Great Plains; the rest of Nebraska and Kansas, the northwestern half of Missouri, and central Oklahoma are in the Central Plains; southeastern Missouri and Oklahoma are in the Interior Uplands.

SALINE HABITATS OF THE CENTRAL UNITED STATES. Saline habitats of the central United States may be divided into two categories having ecological significance for tiger beetles: fluvial, or salty rivers and streams, and nonfluvial. The latter may be arbitrarily subdivided on the basis of size and moisture into small salt patches (usually dry), salt flats (dry or moist), salt marshes, and salt lakes. The two major categories may be in close contact or superimposed, as when salty patches occur next to saline streams or when drainage streams cross large salt flats.

The distribution of saline habitats in the central United States is somewhat irregular. The larger ones occur in a broad band running obliquely from southwestern Oklahoma through central Kansas to southeastern Nebraska. Smaller habitats occur in central and northeastern Oklahoma, southeastern

Kansas, and north-central Missouri. In the central United States, such habitats are usually far isolated from one another compared to parts of the southwestern United States. They are of both natural and man-made origin. In northern Kansas and southern Nebraska, the salt comes from deposits in upper Dakota shales (Cretaceous), while in southern Kansas and northern Oklahoma, the gypsum redbeds (Permian) and Cretaceous strata are responsible (Ungar, 1965; Baalman, 1965). In oil-producing areas, small salty patches or small salt flats frequently occur where brine has been released during drilling. The major oil producing areas of the central United States are found in southeastern and central Kansas and central Oklahoma (Moore and Haynes, 1917; Redfield, 1927).

The man-made saline areas can be dated relatively well. Oil was found in Kansas in 1860, soon after its discovery in Pennsylvania, but most drilling was not done in Kansas and Oklahoma until the late 1800's and early 1900's (Moore and Haynes, 1917; Gould, 1930); thus these saline habitats are not over 80 or 90 years old. Natural saline areas north of the limits of Pleistocene ice (Wright and Frey, 1965) have obviously not existed in their present condition before this time. Frye and Leonard (1952) stated that the present Kansas landscape is a product of erosion and deposition during the Pleistocene.

In pollen analyses of sites in Meade County, Kansas, and Harper County, Oklahoma, Kapp (1963) and Stephens (1959), respectively, concluded that these areas were similar to the present eastern Dakotas or moderate elevations in the southern Rockies during the Illinoian glacial period. Today these areas are short grass prairie.

The physical and chemical conditions of saline habitats are often extreme, particularly at the level at which insects live. Salinity varies greatly with the season (less in spring when most rain occurs), depth (higher at surface), and topography, but may reach as high as 3% (Unger, 1965); when the weather is dry, a white encrustation of crystalline salt usually occurs on the surface. Because of this variability and since tiger beetles occur in most parts of saline habitats, salinity was not measured in this study.

Temperature may be extreme on the bare or sparsely vegetated surface of saline habitats. Geiger (1965) stated that in the summer the surface temperature of bare soil may reach 60, 70, or even 80°C. Above or below the surface the temperature drops rapidly. A study by Sinclair (*in* Geiger, 1965, and Allee *et al*., 1949) in Tucson, Arizona, showed that the soil just below the surface reached 71.5°C, was 62.5°C at a depth of 2 cm, dropped to 42.2°C at 10 cm, and was 20°C at 60 cm; meanwhile the air temperature in a standard shelter was 42.5°C. Also, the daily range of temperatures was greatest near the surface (56.5°C) and less below (40.1°C at 2 cm, 13.8°C at 10 cm, 0°C at 60 cm) or above (31.5°C) the surface. Occasionally measurements of soil and air temperature taken in this study gave similar results; surface temperatures much greater (5-13°C) than air temperatures were frequently noted. Geiger (1965) also stated that a vegetational cover may have a moderating effect on temperature, but what vegetation does occur in saline habitats is usually low and sparse and would have little effect (Geiger said that in grass under a meter high, the maximum temperature is still at the surface).

The availability of water varies considerably with the season as well as with the type of habitat. In rainy weather, saline habitats may be quite moist or flooded, but during the hot, dry months of July and August the surface may become very dry and hard. The salinity of available water varies widely, depending on its origin, and may reach 3% (Ungar, 1965). Humidity also varies greatly; Ortenburger and Bird (1933) noted that the relative humidity on a salt flat at Cherokee, Oklahoma, varied from 80 or 90% in the morning to 20 or 30% at midday.

Wind velocity, usually high in prairies anyway, is especially great on the wide, bare expanses of salt flats. In the summer months the wind normally blows steadily from the south, and on salt flats in southern Kansas and northern Oklahoma, I have estimated the maximum velocity to be 40 to 50 miles per hour during fair weather. Fluvial habitats are usually more protected from wind. The strong wind not only has a physical effect important to flying insects but also has a marked desiccating effect.

Another characteristic of many saline habitats is the general lack of or low amount of cover which would allow insects to escape many of the above conditions as well as predators and parasites.

The vegetation of saline habitats in the central United States is primarily affected by variations in local topography, drainage, and salinity (Ungar, 1965). In most habitats there is an area of very high salinity (2-3%) where no flowering plants occur. In areas of less salinity (up to 2.75%), *Distichlis stricta*, a low, wiry grass, and *Suaeda depressa*, a sparse, succulent chenopod, are the dominant plants. In more marginal and less saline areas, *Atriplex patula* (Chenopodiaceae), *Sporobolus airoides*, *Poa arida*, *Hordeum jubatum*, *Spartina pectinata* (Gramineae), and *Tamarix gallica* (Tamaricaceae, an introduced woody shrub) occur along with the above-mentioned species. Many other species are less common, although some (*Salicornia*, Chenopodiaceae) become dominant species farther west in the United States. More complete analyses of the vegetation of two saline habitats in Kansas and Oklahoma can be found in Ungar (1964, 1965) and Baalman (1965).

On many saline habitats, low mounds or hummocks have been formed by the pioneering vegetation *(Distichlis* and *Suaeda)* collecting blowing sand or soil at their bases. These hummocks may continue to grow, reaching heights of a meter or more in some cases, and allow normal prairie flora and fauna to inhabit their tops (Ortenburger and Bird, 1933; Baalman, 1965).

Some typical saline habitats visited in this study are shown in Figures 1-8.

Fig. 1. Small salty patches in corner of plowed field, 11 m. north, 1 mi. east of Lincoln, Lincoln Co., Kansas (17 June 1963). Fig. 2. Small salt flat near oil wells, 2 mi. north, ½ mi. east of Chanute, Neosho Co., Kansas (18 August 1964). Fig. 3. Small salty patches near Salt Creek, 1 mi. northwest of Fredonia, Wilson Co., Kansas (20 April 1963). Fig. 4. Small intermittent creek with salty banks, 5 mi. north of Yates Center, Woodson Co., Kansas (20 April 1963). Fig. 5. Large (8 miles long, 2 miles wide) salt flat on the Cimarron River, 2.5 mi. southwest of Plainview, Woods Co., Oklahoma (29 August 1963). Fig. 6. Large hummocks on salt flats, Great Salt Plains National Wildlife Refuge, 3 mi. east of Cherokee, Alfalfa Co., Oklahoma (27 August 1963). Fig. 7. Salt marsh with cattails and sedges in area of greatest moisture, ½ mi. east, 1 mi. south of Talmo, Republic Co., Kansas (18 June 1963). Fig. 8. Salt Lake, with bare salty patches around shore, Lincoln, Lancaster Co., Nebraska (19 June 1963).

For the purposes of this paper, most saline habitats can be divided into a central bare, nonvegetated area and a sparsely vegetated marginal area (including the margins of the islandlike hummocks), although in some, the marginal vegetation is tall and dense.

INTRODUCTION TO *CICINDELA*

The genus *Cicindela*[2] is found in terrestrial habitats throughout most of the world from about 50° south latitude to the Arctic Circle, except for high mountains and many midoceanic islands. Except for the closely related monotypic genera *Eurymorpha* and *Apteroessa*, *Cicindela* is considered to be the most highly evolved genus in the family Cicindelidae (Horn, 1926). Many species of *Cicindela* throughout the world live in saline habitats, and many of these are not closely related, hence the ability to live in such habitats has apparently evolved independently a number of times. In general, however, species of saline habitats are among the more highly evolved species of the genus.

Considering the North American fauna of *Cicindela*, many of the more advanced species (the arrangement of Rivalier, 1954, is being followed, with slight modifications) live in saline habitats exclusively, and a sprinkling of less advanced species occur in such habitats occasionally or exclusively. The cicindelids found in saline habitats of the central United States include some species found only in such habitats and some found in both mesic and saline habitats with more or less equal frequency. The species included in this study, with brief notes on their habitat and distribution, are listed in Table 1. As one moves outside the area here arbitrarily called the central United States, other species may be encountered in saline habitats. Some of the species in Table 1 that are primarily found in mesic habitats are relatively uncommon in the habitats studied, and others have been or are being more thoroughly studied by others. Therefore, this study is concentrated on the following species: *C. circumpicta*, *C. cuprascens*, *C. fulgida*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*. In addition, certain other species which are closely related to these will be briefly considered.

BIONOMICS OF *CICINDELA*

The following account is based on observations of several species. Most of the work on the life history was done with *C. togata*, but *C. circumpicta*, *C.*

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[2] A number of workers have suggested splitting *Cicindela* into a variable number of genera. The most recent and best arrangement to date is in a series of papers by Rivalier (1950-1963) based primarily on the male genitalia. This proposal has met some opposition; many workers feel that Rivalier's "genera" should be treated as subgenera. I shall follow the latter viewpoint in this work.

TABLE 1. Species of *Cicindela* included in this study, types of habitats in which they occur, and their general distribution (F=fluvial, N=nonfluvial).

C. circumpicta La Ferté; N (sometimes F) saline habitats; N. Dak., Neb., Mo., Kans., Colo., Okla., N. Mex., Tex., Tamaulipas (Mexico).

C. cuprascens LeConte; F mesic and saline habitats; Manitoba (Canada), Mont., Wyo., Colo., N. Mex., Tex., La., Miss., Ala., Tenn., Ky., Ohio, Ind., Ill., Ia., Minn., and areas enclosed within this circle.

C. duodecimguttata Dejean; F mesic and saline habitats; Northwest Terr. Alberta, Sask., Manitoba, Ontario, Quebec, Labrador, Newfoundland, Nova Scotia, and N. Brunswick (Canada), south to Ga., Ala., Miss., Ark., Tex., Colo., Wyo., Mont., and areas enclosed within this circle.

C. fulgida Say; N saline habitats; Alberta, Sask., and Manitoba (Canada), N. Dak., Mont., S. Dak., Wyo., Neb., Colo., Kans., N. Mex., Okla., Tex., Ariz.

C. hirticollis Say; F mesic and saline habitats; Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, Newfoundland, Prince Edw. Is., and N. Brunswick (Canada), most of continental United States, Baja Calif., Chihuahua, and Vera Cruz (Mexico).

C. macra LeConte; F mesic and saline habitats; Ohio, Ky., Tenn., La., Tex., Colo., Wyo., Neb., S. Dak., Minn., Wisc., Mich., and areas enclosed within this circle.

C. nevadica LeConte; F and N saline (sometimes mesic) habitats; Sonora and Coahuila (Mexico), Calif., Nev., Ariz., Ut., N. Mex., Tex., Okla., Colo., Kans., Neb., Wyo., S. Dak., Mont., N. Dak., Sask. and Manitoba (Canada).

C. punctulata Olivier; N (sometimes F) mesic and saline habitats; Alberta, Sask., Manitoba, and Ontario (Canada), most of continental United States except Pacific Northwest and Calif., Sonora, Chihuahua, Coahuila, Durango, Zacatecas, Hidalgo, Puebla, Distrito Federal, and Mexico (Mexico).

C. repanda Dejean; F and N mesic and saline habitats; Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, Labrador, Newfoundland, N. Brunswick, and Nova Scotia (Canada), most of continental United States except Southwest.

C. schauppi G. Horn; N saline and mesic habitats; Okla., Tex., Nuevo Leon (Mexico).

C. togata La Ferté; N (sometimes F) saline habitats; Neb., Kans., Colo., Okla., N. Mex., Tex., La., Miss., Ala., Fla., S. Car., Tamaulipas (Mexico).

C. tranquebarica Herbst; N mesic and saline habitats; Northwest Terr., Brit. Col., Alberta, Sask., Manitoba, Ontario, Quebec, N. Brunswick, Nova Scotia, and Prince Edw. Is. (Canada), most of continental United States.

C. willistoni LeConte; N (sometimes F) saline habitats; Calif., Nev., Ore., Ut., Ariz., Wyo., N. Mex., Tex., Okla., Kans.

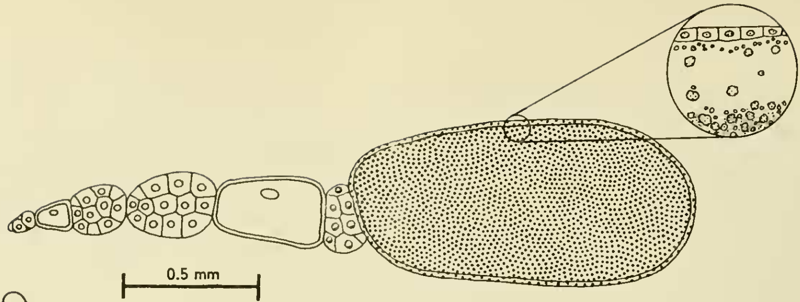
fulgida, and *C. nevadica* were also studied. Nearly all the species in Table 1 were considered from the ecological viewpoint. This account will consider each stage of the life cycle separately. The following brief summary, taken mostly from Balduf (1935), will serve as an introduction to the bionomics of *Cicindela* in general.

The eggs are laid in the soil; the newly hatched first instar larva enlarges the hole produced by the adult's ovipositor into a burrow. Burrows are usually perpendicular to the surface, more or less straight, and with the opening flush with the surface. The three larval instars lie in wait at the entrance to their burrows for prey, the head and pronotum forming a camouflaged "plug" to the burrow. Most small arthropods are accepted as food and are taken to the bottom of the burrow to be consumed unless they are too large for the diameter of the burrow. The last instar larva digs a special pupal cell in which transformation to the adult occurs. The adult digs its way out and spends most of its active hours hunting prey or reproducing. Small arthropods are the usual food. Adults usually prefer open, sparsely vegetated areas and are most active during warm, sunny weather. The female carefully selects the type and moisture of the soil used for oviposition. The length and type of life cycle varies with the species. In some, the adults emerge in the fall, hibernate, and then mate and oviposit in the spring, dying during the summer; in others, the adults emerge during the summer and die before winter. The larval stage occupies most of the life cycle, which may take one to four years to complete.

THE EGG. Since most adult *Cicindela* are about the same size, the eggs of most species are probably very similar. Shelford (1908) said that the eggs of *C. purpurea* and *C. repanda* are about 2 mm long and 1-1.5 mm wide, a translucent creamy yellow, and larger at the anterior end. Moore (1906) gave similar sizes for two eggs of *C. repanda*, but judging from his descriptions, they were apparently atypical and shrunken. Huie (1915) said that the eggs of the European *C. campestris* are 2 mm long, oval, smooth, and yellowish when laid. Ponselle (1900) found the eggs of *C. flexuosa* to be 2 mm long and 1 mm wide.

I found the eggs of *C. circumpicta*, *C. duodecimguttata*, *C. nevadica*, and *C. togata* to be similar. The mean length and width of 38 eggs of *C. togata* measured with an eyepiece micrometer was 2.08 x 1.01 mm; the ranges were 1.85 - 2.43 x 0.92 - 1.12 mm. The average size of four eggs of *C. circumpicta* was 2.21 x 0.99 mm. One egg of *C. duodecimguttata* was 1.80 x 1.14 mm, and a desiccated *C. nevadica* egg was 1.70 x 0.74 mm. Eggs will absorb water and swell slightly if placed in a moist environment. The eggs examined were ovoid and not much larger at the anterior end than the posterior. There is sometimes a slightly concavity on the ventral side. The chorion is shiny, but under high magnification a fine reticulate pattern can be seen. The chorion is not very strong, and the egg is easily ruptured. When first laid, the egg is a creamy or light straw yellow and filled with yolk granules. In *C. togata*, the posterior end of the egg is attached to the soil at the bottom of the hole made by the ovipositor by a short stalk of sticky material (Fig. 13). In *C. circumpicta*, no definite stalk was seen, but the egg adhered to the soil because its posterior end was sticky. Moore (1906), Huie (1915), and Zikan (1929) also noted that *Cicindela* eggs are sticky or fastened by a stalk.

Histological sections of the ovaries of *C. togata* were made and stained



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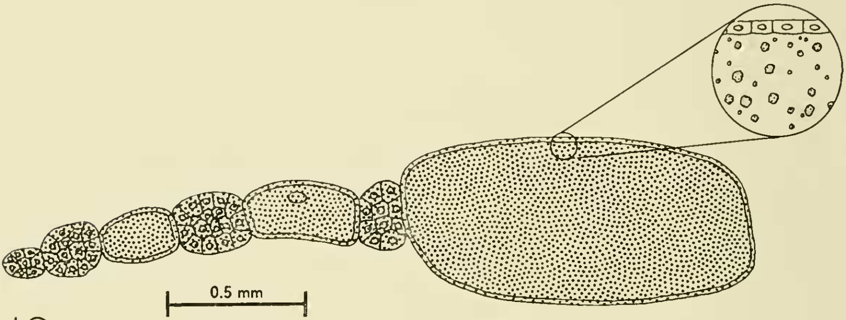

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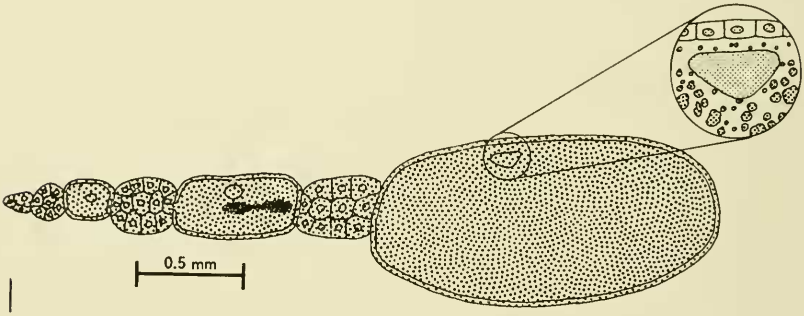

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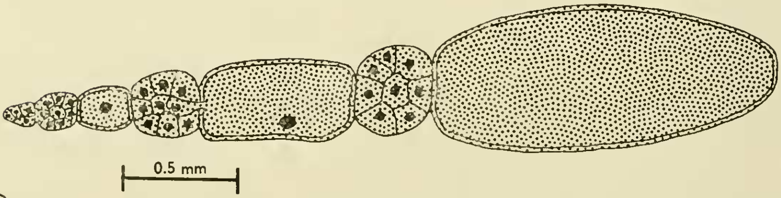

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Figs. 9-12, ovary of *C. togata*, longitudinal section; Fig. 9, stained according to the periodic acid—Schiff procedure; inset: enlargement of the peripheral cytoplasm of the terminal oocyte; areas stained are shaded. Fig. 10, stained according to the azo-coupling protein method; inset: enlargement of the peripheral cytoplasm of the terminal oocyte; areas stained are shaded. Fig. 11, stained according to the Sudan black B method for lipids; inset: enlargement of the peripheral cytoplasm and female pronucleus of the terminal oocyte; areas stained are shaded. Fig. 12, stained according to the methyl green-pyronin Y method for nucleoproteins; areas stained are shaded: black=green, stipple=purple-red.

according to the following methods: the periodic acid-Schiff (PAS) procedure (Barka and Anderson, 1963) for gylcogen, muco- and glycoproteins, glycolipids, mucopolysaccharides, and simple proteins; the azo-coupling protein method (Barka and Anderson, 1963) for proteins in general; the Sudan black B method (Pearse, 1960) for lipids; and the methyl green-pyronin Y method (Pearse, 1960) for nucleoproteins. The results are shown in Figures 9-12. The ovaries of cicindelids are of the polytrophic meroistic type, as are those of all Adephaga (with follicles of nurse cells, or trophocytes, alternating with follicles of oocytes). In Figures 11 and 12, nutrient material can be seen entering oocytes from trophocytes.

In Figure 9, it can be seen that PAS-positive nutrients do not enter the oocyte until very late, since only the terminal oocyte is stained. An enlargement of it shows a layer of cytoplasm near the vitelline membrane with few stained granules. All cells are lightly stained by the azo-coupling reaction (Fig. 10), which is not surprising, since all cells contain proteins. In the terminal oocyte, relatively few granules contain protein. In the Sudan black B lipid reaction (Fig. 11), the cytoplasm of all cells is stained, and the nuclei are only very lightly stained. In the oocyte of intermediate development, a dense-staining central core is present, indicating that most of the lipids have entered the oocyte or have been synthesized within it by this time. This may be the same as the corelike "polar vitelline granules" of Hirschler (1932). In the terminal oocyte, different sized granules are stained in varying degrees, and the nucleus is stained to a greater degree than in other oocytes. In the methyl green-pyronin Y reaction, DNA stains green and RNA stains purple-red. In Figure 12, the nuclei of all cells stained green and the cytoplasm purple-red, as expected.

Embryological Development. The gross embryology of *C. togata* was studied. Fragmentary observations on *C. circumpicta* and *C. duodecimguttata* were similar to those made on *C. togata* and will not be discussed. Almost no work has been done on the embryology of cicindelids. Shelford (1908) published a small drawing of an embryo of *C. purpurea* within the egg and stated that the egg hatches in about two weeks. Huie (1915) mentioned that more mature eggs of *C. campestris* exhibit two pairs of eyes through the chorion. Zikan (1929) said that embryological development takes 9-29 days, depending on the species and temperature (he studied other genera of cicindelids as well as *Cicindela*; the genera *Ctenostoma* and *Odontochila* take about one month).

Eggs of *C. togata* were recovered from terrarium soil in which adults had oviposited. When possible, eggs were dug up just after oviposition. The eggs were kept individually in small covered Stender dishes in which a small amount of water was placed to avoid desiccation. They were examined under a dissecting microscope with transmitted light twice a day. The laboratory

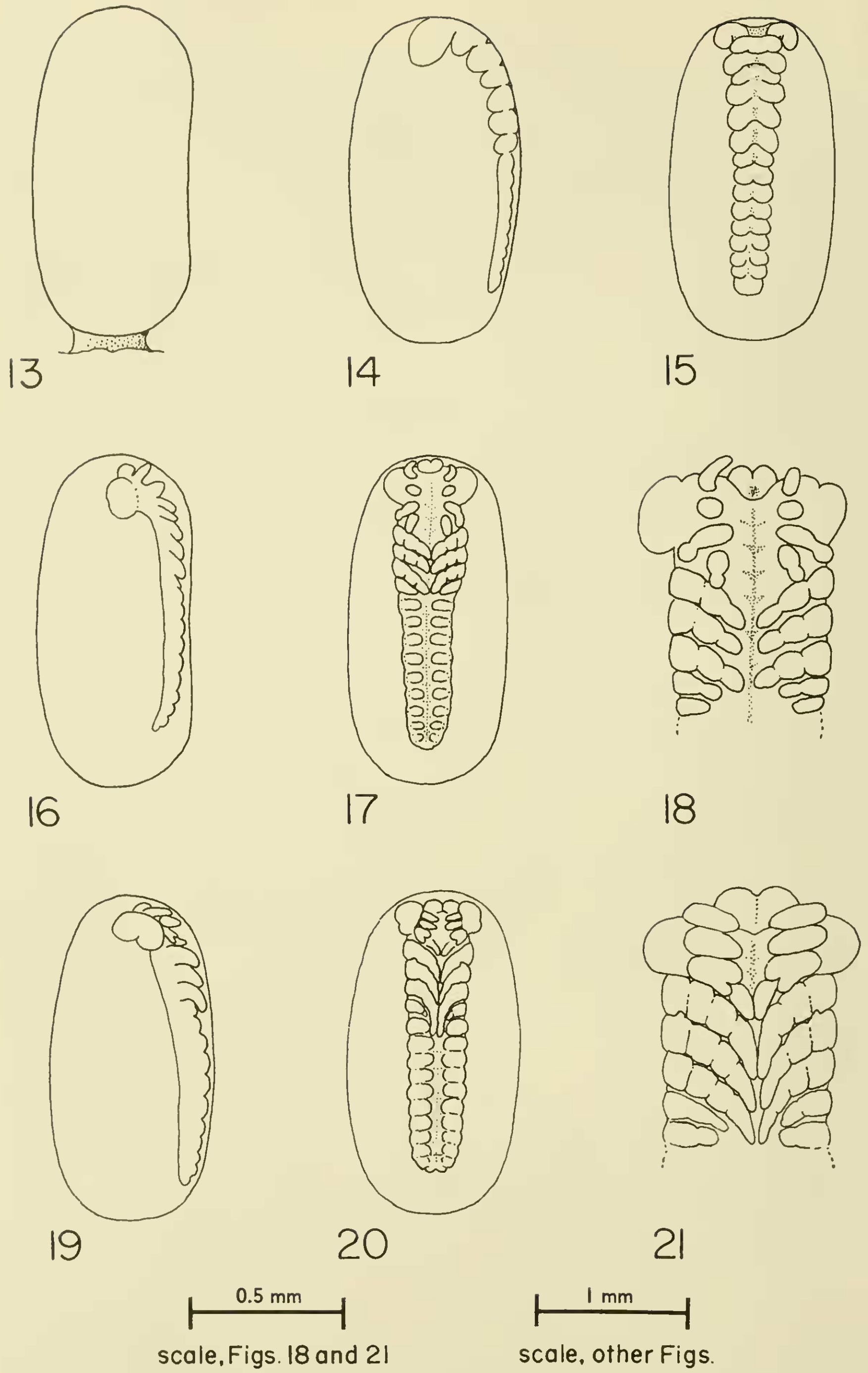
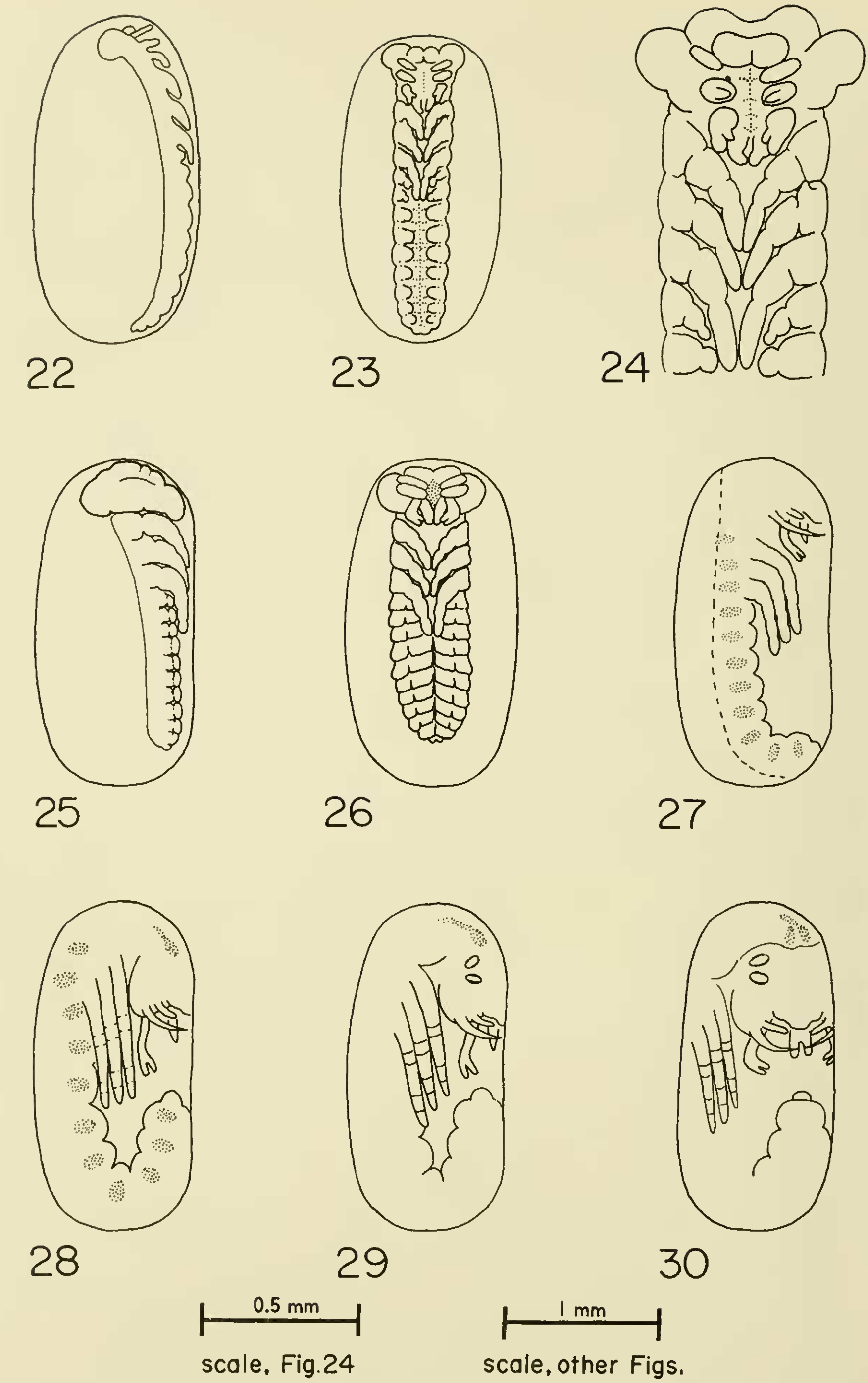


Fig. 13. Newly laid egg of *C. togata*, showing stalk at its posterior end attaching it to the substrate. Figs. 14-21, embryos of *C. togata*; Fig. 14, early embryo (about 1 day old), lateral aspect; Fig. 15, same, ventral aspect; Fig. 16, about 2 days old, lateral aspect; Fig. 17, same, ventral aspect; Fig. 18, same, enlargement of anterior portion; Fig. 19, about 2.5 days old, lateral aspect; Fig. 20, same, ventral aspect; Fig. 21, same, enlargement of anterior portion.

temperature was 24.5°C. The transparent chorion makes eggs of *Cicindela* ideal for such observations. In addition, the embryos of fixed eggs were dissected out and examined.

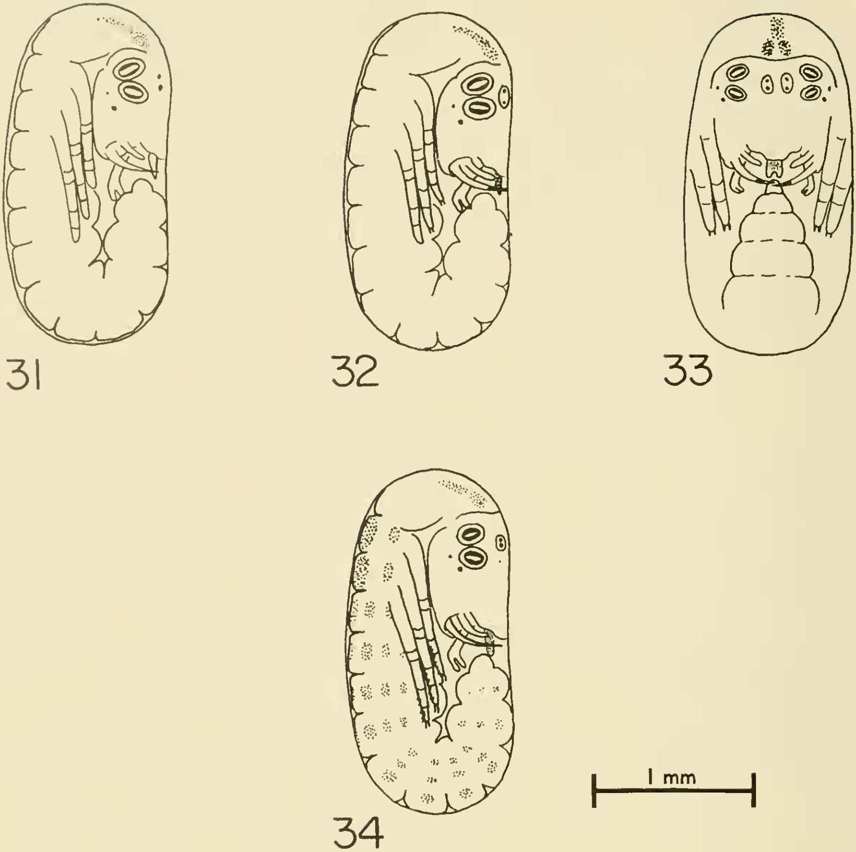
The gross embryological development of *C. togata* is shown in Figures 13-34. The newly laid egg (Fig. 13) is filled with homogeneous appearing yolk granules. Such features as the cleavage center and cleavage nuclei could not be seen. As can be seen in the histological sections (Fig. 11), the female pronucleus is located near the periphery on one side. After about one day, the yolk in the anterioventral portion of the egg appears less dense than the rest (in live eggs). Presumably the germ band and germ layers are being formed or have been formed by this time. Then follow several stages that have been observed only in fixed eggs. Figures 14 and 15 show an early embryo. Head and thoracic segmentation are well developed, and abdominal segmentation is nearly complete. Only four segments can be seen in the head region, the apical one being composed of the paired lateral lobes. A median line, or primitive groove, is just beginning to develop midventrally. At a later stage (Figs. 16-18), the lateral lobes of the head are much enlarged; four pairs of head appendages (antennae, mandibles, maxillae, and labium) plus a median bilobed labral bud are clearly visible; the maxillae and labium are beginning to segment; what is probably the stomodeum can be seen as a depression at the base of the labral bud. The thoracic and first abdominal appendages are quite long and are beginning to segment; other abdominal appendages are mere bumps. The median line is clearly evident. At a slightly later stage (Figs. 19-21), the head appendages have enlarged and thickened; the maxillae are beginning to become bilobed; the labial appendages have moved closer together. The thoracic and first abdominal appendages are clearly segmented, and the other abdominal appendages are beginning to segment. The legs are longer. The fifth abdominal segment is slightly larger in diameter than those surrounding it. Slightly later (Figs. 22-24), the head appendages have elongated; the mandibles begin to assume their future scimitar shape; the outer lobes of the maxillae have elongated considerably; what may be the anterior tentorial pits can be seen at the bases of the mandibles when the antennae are straightened out. The first abdominal appendage is three-segmented, and the other abdominal appendages are slightly two-segmented. At this stage the early embryo has reached maximum elongation. Later, when the embryo is about three to four days old (Figs. 25, 26), the lateral lobes of the head have enlarged greatly; the maxillae have assumed a characteristic L shape. The legs are longer, but the body is shorter and wider. The abdominal appendages have begun to regress. Returning to observations of living eggs, Figure 27 shows a stage slightly more advanced (4 to 5.5 days old) than that in Figures 25 and 26. The amount of yolk has decreased considerably; the embryo has



Figs. 22-30, embryos of *C. togata*; Fig. 22, about 3 days old, lateral aspect; Fig. 23, same, ventral aspect; Fig. 24, same, enlargement of anterior portion; Fig. 25, about 3.5 days old, lateral aspect; Fig. 26, same, ventral aspect; Fig. 27, about 4-5.5 days old, lateral aspect; Fig. 28, about 5-6.5 days old, lateral aspect; Fig. 29, about 7-9 days old, lateral aspect; Fig. 30, same, ventrolateral aspect.

moved dorsally; and the abdomen is beginning to flex ventrally. The mandibles are much elongated and clearly sickle-shaped, and the L-shaped, bilobed maxillae are much longer. Dark segmental "spots" can be seen internally in the thorax and abdomen. A paired pulsating organ appears in the anterior region of the prothorax. During the next day, the body continues to elongate, forcing the head and abdomen closer together (Fig. 28). The abdomen may be seen moving slightly. At an age of 7 to 9 days, the body is slightly longer, and two pairs of large developing stemmata become visible as very faint orange ovals on either side of the head (Figs. 29, 30). A tubular pulsating area can be seen extending posteriorly through the thoracic region from the paired organ near the head. The internal segmental "spots" are no longer visible. Probably the dorsal closure is completed by this stage. In another day (8 to 10 days days after oviposition), the large ovals representing developing stemmata have become thicker and dark orange; three additional pairs of smaller stemmata become visible as faint gray dots, two pairs mesad of the large pairs and one pair laterad of the most posterior large pair; the large pairs of developing stemmata are surrounded by transparent circles. The dorsal segmentation can be clearly seen. What appears to be the labium becomes light orange (Fig. 31). The entire embryo may move slightly in this and subsequent stages. About one day later (Figs. 32, 33), the small pairs of stemmata are darker gray, and another pair is beginning to develop laterad of the posterior large pair; the median pairs of small stemmata have transparent circles around them. The labium is dark orange; the tips of the mandibles (but not the extreme tips) are orange; the tarsal claws of the first legs are orange and those of the second legs light orange. A few hours to one-half day later (Fig. 34), the stemmata mentioned above are darker orange (large ones) or gray (small ones); the two pairs of medial stemmata have begun to fuse (the anterior ones with the posterior) and each fused pair is surrounded by a common transparent circle; another medial pair of stemmata is visible posterior to the fused pairs as very light gray dots. The orange of the mandibles has spread slightly; the tarsal claws of the second legs are orange, and those of the third legs are light orange. Sclerites of the legs, thorax, and abdomen are very light gray; the setae at the apical ends of the legs are dark. When development reaches this stage, the larva bursts the chorion at the anterior end and in about five minutes, wiggles out. The duration of embryological development, measured in four individuals, is from 10.5 to 11.25 days under laboratory conditions (temperature 24.5°C).

THE LARVA—*Descriptions.* The larvae of cicindelids are relatively little known, either biologically or taxonomically. A number of workers have described many of the palearctic species, and the larvae of some tropical genera are known. Among the more important papers for these regions are van Emden (1935, 1943), Zikan (1929), Friederichs (1931), Blair (1920), Hamil-



Figs. 31-34, embryos of *C. togata*; Fig. 31, about 8-10 days old, lateral aspect; Fig. 32, about 9-11 days old, lateral aspect; Fig. 33, same, ventral aspect; Fig. 34, just before eclosion, lateral aspect.

ton (1925), and Gilyarov and Sharova (1954). In North America, G. Horn (1878) described one species in each of the four North American genera; Schaupp (1879a) listed the species that had been described at that time; Shelford (1908) described rather superficially the larvae of 12 species; Hamilton (1925) described in detail 28 North American and six palearctic species of *Cicindela*, three species of *Megacephala*, three species of *Omus*, one species of *Amblychila*, and two species of tropical genera, and standardized the morphological terminology; Ortenburger and Bird (1933) published crude drawings of the larva of *C. willistoni* and the fifth abdominal segment of the larvae of *C. cuprascens* and *C. togata*; Spangler (1955) described the larva of *C. circumpicta*, but his drawings do not show some important details and are incorrect in others.

In this study, the larvae of six species were collected; four were identified by rearing and two *(C. fulgida* and *C. willistoni)* by the process of elimination. One of these, *C. duodecimguttata*, has been adequately described by Hamilton (1925) and will not be described here; the larvae of *C. togata*, *C. nevadica*, *C. fulgida*, and *C. willistoni* are described for the first time, and *C. circumpicta* is redescribed. See Hamilton (1925) for an explanation of morphological terminology. Descriptions of larval cicindelids have traditionally been based on last instar larvae, no doubt partly because of a scarcity of specimens of younger instars. I shall follow this convention, although I have also collected or reared first and second instar larvae of most of the species described here.

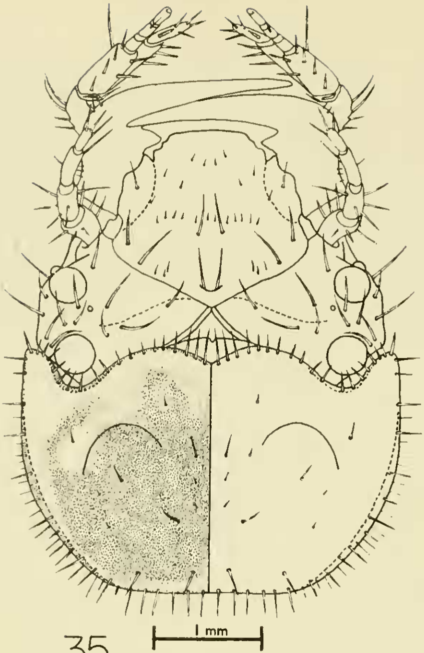
Larvae will be deposited in the following institutions: U.S. National Museum (all five species), American Museum of Natural History (all species except *C. fulgida*), and The University of Kansas (all species except *C. fulgida* and *C. willistoni*).

C. circumpicta johnsoni Fitch—third instar larva (Figs. 35-40)

Color. Head cupreous, cupreous-green, brassy green, or blue, with green, blue-green, blue, or purple reflections; labrum red-brown with black margin; pronotum with most of disk chestnut brown in a pattern which may be more or less developed (Fig. 35); cephalolateral angles yellow-brown to yellow; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antennal segments yellow-brown, distal segment reddish brown, penultimate segment intermediate; mandibles reddish brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum medium in length and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area slightly wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.85 as long as penultimate, proximal segment slightly longer than second segment, proximal segment with 6-7 setae, second with 7-9, third with 3-4, and distal with 3-5; maxillae with 3 setae on mesal margin of proximal segment of galea and 4-5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 2 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae medium in length; secondary setae few, 5 or 6 pairs.



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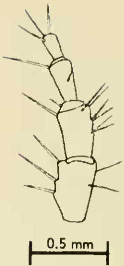

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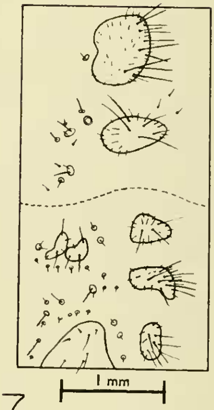

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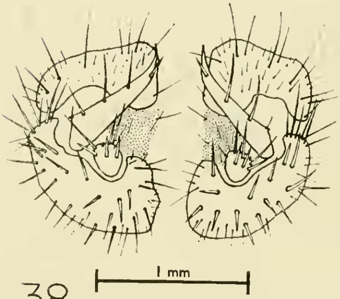

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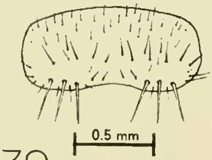

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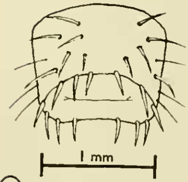

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Figs. 35-40, *C. circumpicta johnsoni*, third instar larva; specimen is from Geuda Springs, Sumner Co., Kansas; Fig. 35, head and pronotum, dorsal aspect; left half of pronotum shaded to show the pattern; Fig. 36, left antenna, ventral aspect; Fig. 37, third abdominal segment, lateral aspect of left half, with the middorsal line at top and midventral line at bottom; ventrolateral suture dotted; Fig. 38, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 39, ninth abdominal sternum, ventral aspect; Fig. 40, pygopod, dorsal aspect.

Abdomen. Sclerotized areas distinct, supplementary lateral sclerotized areas variable in number and shape; secondary setae numerous, some long and slender, some short and fine; eusternum of ninth segment bearing 2 groups of 3 long setae caudally; pygopod usually bearing 14 setae, 7 on a side; median hooks of fifth segment with 4-5 (rarely 6) setae, the distal one stout and directed mesad, the others more slender and directed laterad; inner hooks with 6-8 setae, 3-5 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 16-21 mm; width at third abdominal segment, about 2 mm; diameter of stemma I, 0.34-0.38 mm; diameter of stemma II, 0.27-0.37 mm; distance between stemmata I and II, 0.21-0.30 mm; length of fronto-clypeo-labral area, 1.5-1.7 mm; width of fronto-clypeo-labral area, 1.56-1.80 mm; length of pronotum, 1.93-2.19 mm; width of pronotum, 2.93-3.25 mm.

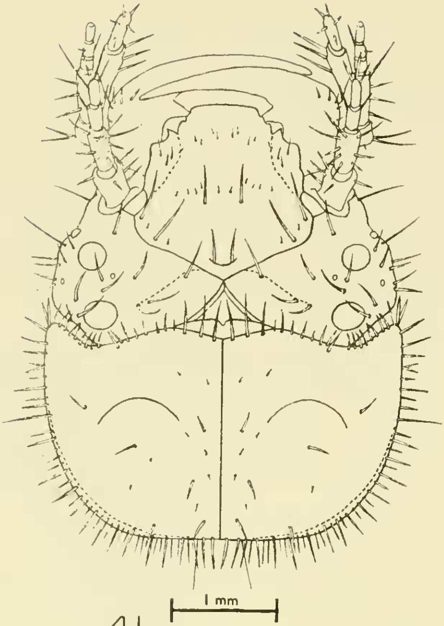
C. fulgida fulgida Say—third instar larva (Figs. 41-46)

Color. Head red-brown with brassy green and cupreous-purple reflections; labrum red-brown with black margin; pronotum brown or dark red-brown with cupreous-purple reflections; cephalolateral angles lighter brown; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; antennae red-brown; mandibles red-brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae white, other setae yellow-brown.

Head. Setae on dorsum medium in length; diameter of stemma II noticeably smaller than that of stemma I and smaller than distance between I and II; fronto-clypeo-labral area slightly longer than wide; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.7 as long as penultimate, proximal segment shorter than second segment; proximal segment with 5-6 setae, second with 9, third with 2, and distal with 3-4; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 2 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending cephalad slightly more than mesal portion; lateral angles carinate; primary setae medium in length; secondary setae few, 7 or 8 pairs.

Abdomen. Sclerotized areas distinct; secondary setae numerous, most long and slender, a few short; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 18 setae, 9 on a side; median hooks of fifth segment with 2 setae; inner hooks with 2 setae on a shoulder and long spine over one-third the length of the hook.



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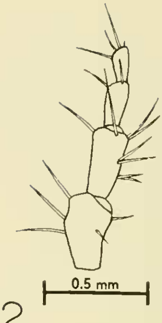

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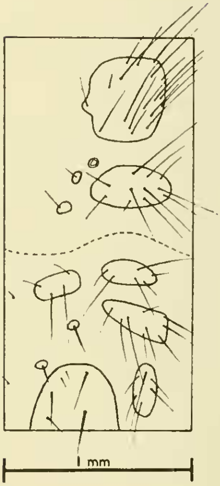

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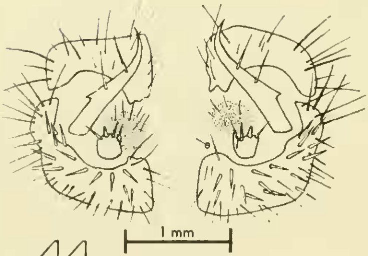

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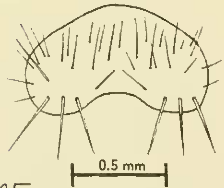

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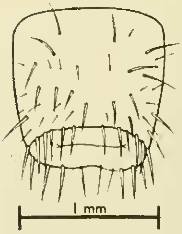

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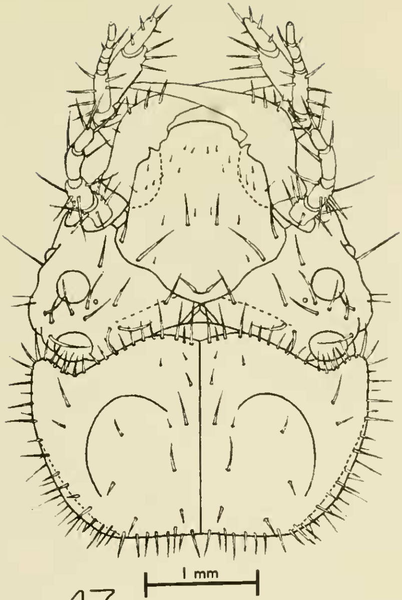
Figs. 41-46, *C. fulgida fulgida*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 41, head and pronotum, dorsal aspect; Fig. 42, left antenna, ventral aspect; Fig. 43, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; Fig. 44, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 45, ninth abdominal sternum, ventral aspect; Fig. 46, pygopod, dorsal aspect.



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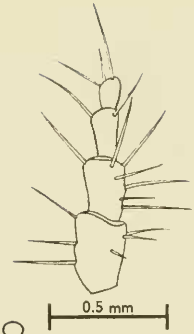

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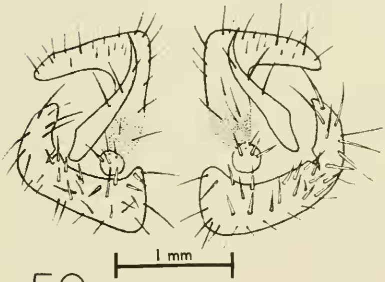

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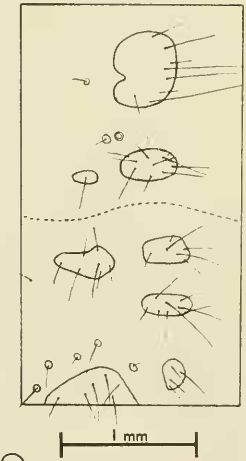

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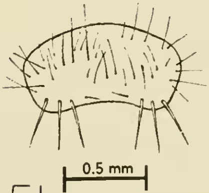

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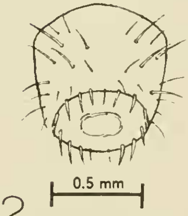

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Figs. 47-52, *C. nevadica knausi*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 47, head and pronotum, dorsal aspect; Fig. 48, left antenna, ventral aspect; Fig. 49, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; Fig. 50, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 51, ninth abdominal sternum, ventral aspect; Fig. 52, pygopod, dorsal aspect.

Measurements. Total length of larva, 14-18 mm; width at third abdominal segment, 1.7 mm; diameter of stemma I, 0.30 mm; diameter of stemma II, 0.26 mm; distance between stemmata I and II, 0.28 mm; length of fronto-clypeo-labral area, 1.48 mm; length of pronotum, 1.83 mm; width of pronotum, 2.95 mm.

C. nevadica knausi Leng—third instar larva (Figs. 47-52)

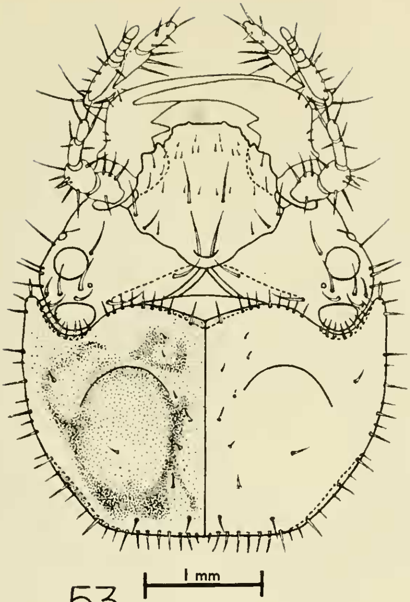
Color. Head black with metallic blue-green, green, purplish, or sometimes bronze reflections; labrum red-brown; pronotum with cephalolateral angles red-brown and disk black with purple, blue-green, brassy, and cupreous reflections; mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; antennae reddish brown; mandibles reddish brown basally with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum prominent, long to short; diameter of stemma II subequal to that of stemma I and greater than distance between I and II; fronto-clypeo-labral area slightly wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.6 as long as penultimate; proximal and second segments about equal in length; proximal segment with 6-9 setae, second with 8-9, third with 2, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate segment with 2 large and one reduced spur and two setae on either side of spurs; ligula with 3 setae.

Thorax. Pronotum with cephalolateral angles not extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae long to short; secondary setae few, 4 to 6 pairs.

Abdomen. Sclerotized areas distinct; secondary setae few, some very long and slender, some medium in length; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 14 setae, 7 on a side; median hooks of fifth segment with 3-4 setae, all of about the same diameter; inner hooks with 4-5 setae, 3 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 18-20 mm; width at third abdominal segment, about 2 mm; diameter of stemma I, 0.31-0.33 mm; diameter of stemma II, 0.27-0.33 mm; distance between stemmata I and II, 0.22-0.26 mm; length of fronto-clypeo-labral area, 1.42 mm; width of fronto-clypeo-labral area, 1.44-1.48 mm; length of pronotum, 1.57-1.72 mm; width of pronotum, 2.43-2.63 mm.



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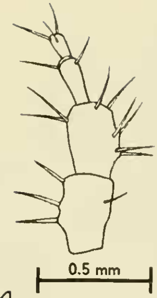

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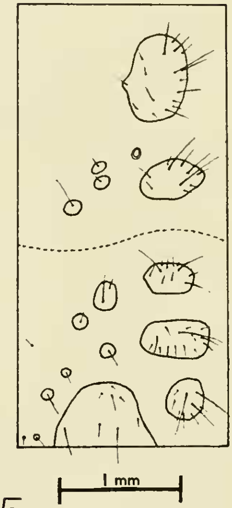

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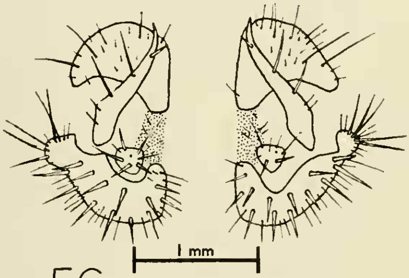

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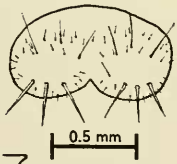

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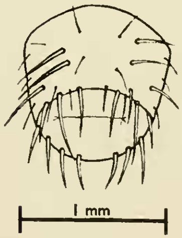

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Figs. 53-58, *C. togata globicollis*, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 53, head and pronotum, dorsal aspect; left half of pronotum shaded to show pattern; Fig. 54, left antenna, ventral aspect; Fig. 55, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; Fig. 56, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; Fig. 57, ninth abdominal sternum, ventral aspect; Fig. 58, pygopod, dorsal aspect.

C. togata globicollis Casey—third instar larva (Figs. 53-58)

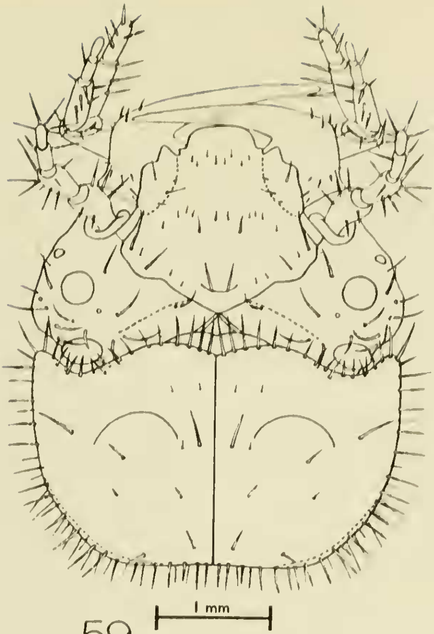
Color. Head cupreous and green with green reflections; labrum red-brown with 2 opalescent white spots and black margin; angulus frontalia opalescent white; pronotum with white margin, disk with pattern of red-brown to yellow-brown on yellow-brown to yellow background, which may be more or less developed (Fig. 53); mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antennal segments opalescent white, distal two segments yellow-brown; mandibles reddish brown basally, with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae transparent, other setae yellow-brown.

Head. Setae on dorsum short and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area wider than long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.57 as long as penultimate, proximal segment equal in length to second segment; proximal segment with 6 setae, second with 8-9, third with 3, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimae segment of palpus with 2 setae; distal segment of labial palpus with 1 ventral seta, penultimate with 3 spurs and 3 setae on either side of spurs; ligula with 4 setae.

Thorax. Pronotum with cephalolateral angles extending cephalad as far as or slightly beyond mesal portion; lateral margins slightly carinate; primary setae short; secondary setae few, 2 to 4 pairs.

Abdomen. Sclerotized areas distinct, supplementary lateral sclerotized areas variable in number and shape; secondary setae fairly numerous, some long and slender, some short and fine; eusternum of ninth segment bearing 2 groups of 3 long setae caudally; pygopod usually bearing 12 setae, 6 on a side; median hooks of fifth segment with 4-5 setae, the distal one stout and directed mesad, the others more slender and directed laterad; inner hooks with 5-8 setae, 3-5 of which are notably stouter than the others; spine of inner hooks minute to obsolete.

Measurements. Total length of larva, 17-19 mm; width at third abdominal segment, about 1.9 mm; diameter of stemma I, 0.32-0.35 mm; diameter of stemma II, 0.27-0.34 mm; distance between stemmata I and II, 0.23-0.27 mm; length of fronto-clypeo-labral area, 1.28-1.35 mm; width of fronto-clypeo-labral area, 1.42-1.50 mm; length of pronotum, 1.83-2.08 mm; width of pronotum, 2.85-3.20 mm.



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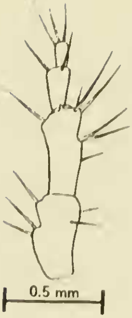

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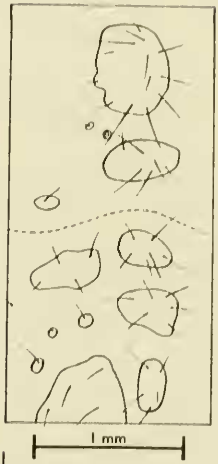

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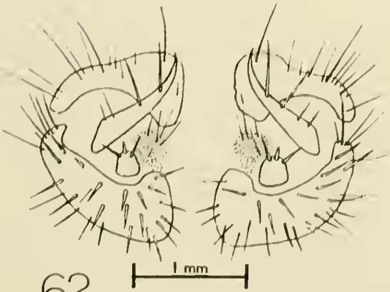

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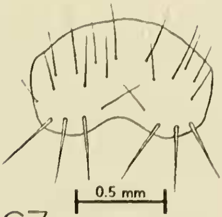

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FIGS. 59-64, *C. willistoni*, new subspecies, third instar larva; specimen is from 11 mi. northeast of Hudson, Stafford Co., Kansas; FIG. 59, head and pronotum, dorsal aspect; FIG. 60, left antenna, ventral aspect; FIG. 61, third abdominal segment, lateral aspect of left half; ventrolateral suture dotted; FIG. 62, dorsum of fifth abdominal segment, dorsal aspect; stippled area is weakly sclerotized; FIG. 63, ninth abdominal sternum, ventral aspect; FIG. 63, pygopod, dorsal aspect.

C. willistoni, new subspecies, described later—third instar larva (Figs. 59-64)

Color. Head dark brown to red-brown with brassy, green, blue-green, or purplish reflections; labrum red-brown; pronotum with disk usually dark red-brown (rarely red-brown in a pattern), with cephalolateral angles red-brown (rarely yellow-brown); mesonotum dark brown anteriorly, yellow-brown posteriorly; metanotum yellow-brown; basal two antenna segments red-brown to yellow-brown, distal two segments red-brown; mandibles reddish brown basally, with apices and retinaculum black; maxillae and labium yellow-brown. Dorsal cephalic and pronotal setae white, other setae yellow-brown.

Head. Setae on dorsum medium to short and prominent; diameter of stemma II subequal to that of stemma I and slightly greater than distance between I and II; fronto-clypeo-labral area about as wide as long; U-shaped ridge on caudal part of frons with 2 setae; antennae with distal segment 0.6 to 0.7 as long as penultimae; proximal segment shorter than second segment; proximal segment with 5-6 setae, second with 9-10, third with 2, and distal with 3; maxillae with 3 setae on mesal margin of proximal segment of galea and 5 on distal segment; maxillary palpus 3-segmented, palpifer with 7 setae, penultimate segment of palpus with 1 seta; distal segment of labial palpus with 1 ventral seta, penultimate segment with 3 spurs and 2 setae on either side of spurs; ligula with 4 (occasionally 6) setae.

Thorax. Pronotum with cephalolateral angles not extending as far cephalad as mesal portion; lateral margins slightly carinate; primary setae medium to short, secondary setae few, 3 to 4 pairs.

Abdomen. Sclerotized areas distinct, secondary lateral sclerotized areas variable in shape; secondary setae few, some long, some short; eusternum of ninth segment bearing 2 groups of 3 long and 1 shorter seta caudally; pygopod usually bearing 16 setae, 8 on a side; median hooks of fifth segment with 3-4 setae; inner hooks with 2 setae on a shoulder, spine long, over one-third the length of the hook.

Measurements. Total length of larva, 18 mm; width at third abdominal segment, about 2.3 mm; diameter of stemma I, 0.30-0.35 mm; diameter of stemma II, 0.27-0.34 mm; distance between stemmata I and II, 0.24-0.35 mm; length of fronto-clypeo-labral area, 1.42-1.70 mm; width of fronto-clypeo-labral area, 1.42-1.76 mm; length of pronotum, 1.66-2.02 mm; width of pronotum, 2.56-3.03 mm.

The larvae of *C. fulgida* and *C. willistoni* are segregated to couplet 7 in Hamilton's (1925) key; they can be separated from the species in that couplet by the following key:

1. Setae of dorsum of head and pronotum brown .... *sexguttata*
   Setae of dorsum of head and pronotum white 2

2. Median hooks of fifth abdominal segment with two setae .... *fulgida*
   Median hooks of fifth abdominal segment with more than three setae 3
3. Antennal scape shorter than pedicel .... *willistoni*
   Scape and pedicel of antenna subequal in length .... *campestris*

The larvae of *C. circumpicta*, *C. nevadica*, and *C. togata* are segregated to couplet 24 in Hamilton's (1925) key; they can be separated from the species in that couplet by the following key:

1. Inner hooks of fifth abdominal segment with nine or ten setae .... *marginata*
   Inner hooks of fifth abdominal segment with fewer than nine setae 2
2. Scape and pedicel of antenna opalescent white .... *togata*
   Scape and pedicel of antenna brown 3
3. Antennal pedicel with ten to 12 setae .... *abdominalis*
   Antennal pedicel with fewer than ten setae 4
4. Cephalolateral angles of pronotum not extending as far cephalad as mesal portion; pronotum less than 2.7 mm wide .... *nevadica*
   Cephalolateral angles of pronotum extending as far cephalad as mesal portion; pronotum more than 2.8 mm wide .... *circumpicta*

THE LARVA—*Bionomics.* Many brief notes and papers have appeared concerning the bionomics of cicindelid larvae, some of which will be mentioned later. Among the more important are Zikan's (1929) large paper on South American species, Shelford's (1908) paper, Huie's (1915) work on *C. campestris*, Friederich's (1931) detailed study of eyes, and two papers by Criddle (1907, 1910).

Sclerotization. The first instar larva of *C. togata*, upon hatching, is about 3 mm long. The body is light straw yellow except for the tips of the mandibles and the large stemmata, which are orange, and the meso- and metathoracic, abdominal, and leg sclerites and the small stemmata, which are light gray. The two hind pairs of legs are slightly darker gray than the front legs. After about four hours the above mentioned sclerites are darker gray, and the dorsum of the head and parts of the pronotum are gray. The gray of the mandibles has spread basally to about half their length. In about six more hours, the body sclerites are gray-brown, and the top of the head is dark and iridescent cupreous and green. The venter of the head is light brown. The mandibles are almost entirely black. In about 15-24 hours after eclosion, the larva is complete sclerotized. The abdominal sclerites are light gray-brown; the thoracic and leg sclerites (except the pronotum) are dark gray-brown; the pronotum is light yellow-brown with a darker brown pattern; the dorsum of the head is dark brown with cupreous and green reflections; the venter of the head is orange-brown; the mandibles are black; and the other head appendages are light-brown.

Burrows and digging. In nature, after the first instar larva is sclerotized, and if the soil is moist enough, it enlarges the cell that contained the egg into a burrow. Shelford (1908) said that the larva of *C. purpurea* first digs the burrow from the depth of the egg to the surface, then digs beneath this to a depth of 10-15 cm. The exact method of digging the first burrow was not determined in this study. The effect of soil moisture was noted in the laboratory terraria. Soil that had begun to dry out was watered, and shortly afterward numerous first instar larval burrows began to appear. If the soil becomes too dry again, the larva plugs the burrow with soil, apparently to conserve moisture.

In digging a burrow, the larva (of all instars; third instars are described here), head downward, loosens some soil with its mandibles, using its legs for support. Then the anterior end of the body is bent around in the other direction, and the head and pronotum are placed shovellike under the loose soil. The larva finishes turning right-side-up in the burrow and elevates the soil up the burrow on top of its head and pronotum. Upon reaching the surface, the larva may flip its head and pronotum backward, throwing the soil several centimeters away (if the soil is moist and sticky, it is deposited in the form of small pellets). Some species pack the soil around the entrance of the burrow by turning the head upside down and pushing with the legs. When the larva is beginning a burrow from the surface, as when it is introduced into a jar of soil in the laboratory, slightly different tactics are used. The thorax is humped, the larva supported by its front and especially hind legs (the middle legs are normally held horizontally from the body to help support the larva in the center of the burrow and are useless for walking when it is outside the burrow), in order to allow the mandibles, which slant upward from the head, to dig into the soil. When the hole is about 1 cm deep, the larvae may hold the abdomen in the air while using the legs to gain leverage. The larva uses the method of digging upside down and backing out the hole to flip the soil away until the hole is about 2 cm deep. At depths below that, the method of turning around in the burrow, described above, is used. The temporary bottom of the burrow is made slightly larger than the finished diameter; soil is later "plastered" on the walls as the burrow descends. When the burrow is completed, the larva clears the soil around the entrance of all movable obstructions within a distance of about half its body length, forming a slightly concave smooth area. Some of the same observations on digging have been made by Criddle (1907), Fackler (1918), Enock (1903), and Macnamara (1922). Shelford (1908) noted an exception: the burrow entrance of *C. macra* is ragged at the edge, rather than smooth. Some authors (Macnamara, 1922; Bryson, 1939) have noted an increase in burrowing activity after rains, and Criddle (1907, 1910) noted that most digging is done at night except late in the season when the nights are cold.

The depth of the burrow varies with many factors, including the instar, species, weather and climate, season, soil moisture, and possibly type of soil.

Shelford (1908) gave depths of (presumably) third instar burrows of eight species ranging from 5-90 cm, depending on the species, temperature, and possibly soil moisture. Criddle (1907, 1910) gave depths for six species ranging from 15-200 cm, depending on the instar, species and season (larvae deepen their burrows before hibernation). Zikan (1929) showed burrow depths of the species he studied. The depths of burrows measured in this study are shown in Table 2.

Table 2. Depths of larval burrows measured (in cm.) in the field (F) and laboratory (L).

	Instar		
Species	First	Second	Third
C. circumpicta	6.5-9 (F)	13.5-16.5 (F)	11-29.5 (F)
			6-14 (L)
C. duodecimguttata	1.5-3.5 (F)	3.5-4.5 (F)	
	2-2.6 (L)	4 (L)	6-11 (L)
C. fulgida		13 (F)	
C. nevadica		18-28 (F)	22-35 (F)
C. togata	2.5-4 (F)	6.5-10 (F)	10-18 (F)
	5 (L)		10-35 (L)
C. willistoni	7-13 (F)	12 (F)	16-35 (F)

The diameter of most larval burrows is slightly greater than the diameter of the head and pronotum, although Zikan (1929) and Williams and Hungerford (1914) showed the terminal part of the burrows of some species of other genera as being enlarged, and Shelford (1911) showed a similar burrow of *C. limbalis.* The larva can easily turn around inside the burrow. In doing this it bends the anterior end of the body dorsally using the legs, forcing the head past the dorsum of the abdomen (Shelford, 1911).

The burrows of most species are approximately straight and perpendicular to the soil surface, which may be vertical, horizontal, or oblique. However, there are many exceptions and much intraspecific variation. Burrows that I have dug up in the field or laboratory are aften curved, oblique to the surface, or both. Such variations have also been shown by some of the above authors as well as Hood (1903). Reineck (1923) noted that the larvae of *C. silvicola* will dig around large obstructions in their path.

The burrows of many species open flush with the surface or with a slight depression as noted above, but others are quite different. Shelford (1908) noted that the burrow of *C. lepida,* which is found in dry sand, has a funnel at the entrance formed by the action of gravity on the sand. Ortenburger and Bird (1933) noted similar craterlike entrances to burrows of *C. cuprascens.* Shelford (1908) and Criddle (1910) found that *C. formosa* builds a pit about 4 cm wide and 2.5 cm deep. From about half way up one side, the burrow begins horizontally, then curves downward. Similar burrows were noted by Dow (1916) for four species, including *C. lepida* and *C. scutellaris.* However, he did not collect larvae for identification, but used the uncertain method of placing wire screen cages over the burrows to catch the emerging adults (uncertain because the adult does not necessarily dig its way out along the old larval burrow; larval burrows of different species may be close together, and the adult from one may emerge near another). Dow's determinations are thus in doubt, since Shelford (1908) and I have noted different burrow entrances for *C. lepida* and *C. scutellaris*, respectively.

Lesne (1897, 1921) and Reineck (1923) reported that *C. hybrida* and *C. silvicola*, which burrow in sloping areas, build a semicircular lip above the entrance (apparently to deflect rain) and a pit below the entrance.

Shelford (1908) said that *C. limbalis* builds a chimneylike structure about 6 mm high at the entrance. Macnamara (1922) stated that the larvae of *C. tranquebarica* build a similar structure when necessary, as when an immovable obstruction is present. Hamilton (1925) said that an unidentified species from Colorado builds a chimney about 2.5 cm high in its early instars. Zikan (1929) showed a similar structure on a burrow of *Megacephala brasiliensis.* A second instar burrow of *C. fulgida* that I found in northern Kansas was situated among dead *Distichlis* stems; the larva had built a chimney about 0.5 cm high to elevate the entrance above these obstructions (other burrows of the same species had no such structure). This chimney-building habit is best developed in *C. willistoni.* Ortenburger and Bird (1933) first noticed this phenomenon in Oklahoma, but did not know which species is involved; I have studied it in Oklahoma and Kansas (in a new subspecies). In this species the larva always builds a chimney (called a turret by Ortenburger and Bird) relatively much higher than any other *Cicindela* known and adds two projections at the top, giving the apex a saddlelike appearance (Figs. 65-67). First instar turrets are usually 1-3 cm high; second and third instar turrets are 1.5-4 cm high (one second instar turret was 5.5 cm high). The apical projections have no special orientation. In the laboratory, larvae build shorter turrets and never add the projections. The function of these turrets is uncertain. They do not seem to serve for flood protection since they crumble in a heavy rain. Another possibility is to elevate the larva above the surface, which is the hottest part of the environment; however, when conditions become very hot and dry, the larvae usually plug their burrows and remain underground. A third possibility is that some insects that could serve as prey may be attracted to such projections as landing places.

At various times (after feeding, in unfavorable weather, before hibernation or estivation, before molting or pupation) the larva may close the burrow with a plug of soil. This is done by scooping a small amount of soil from the

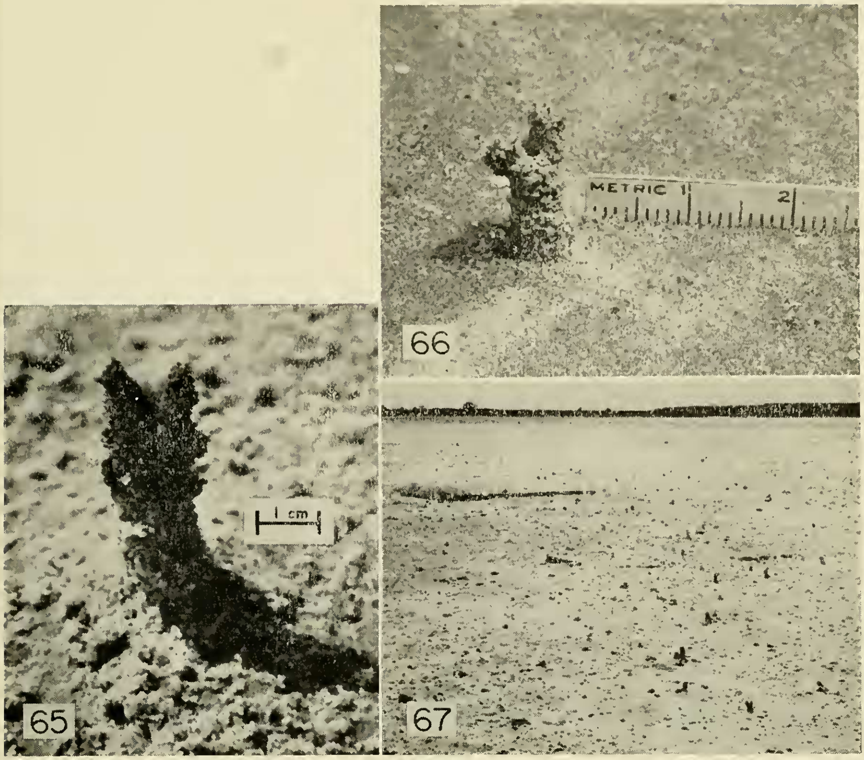


Fig. 65. Turret of third instar larva of *C. willistoni*, 2.5 mi. southwest of Plainview, Woods Co., Oklahoma. Fig. 66. Turret of second instar larva of *C. willistoni*, 11 mi. northeast of Hudson, Stafford Co., Kansas. Fig. 67. View of a number of turrets of larvae of *C. willistoni* on salt flat 2.5 mi. southwest of Plainview, Woods Co., Oklahoma; insect net is about 1 m long.

wall or bottom of the burrow onto the head and applying it to the entrance repeatedly. The burrow is unplugged in reverse fashion, the soil from the plug being plastered onto the walls. The thickness of the plug varies from less than one to several centimeters; it is thicker if the larva spends long periods underground (hibernation, pupation, etc.). I have noticed that the larvae in terraria often plugged their burrows temporarily soon after the soil was moistened. In nature this reaction probably saves their burrows from being flooded during rains.

Because the burrow diameter is nearly the same size as the head width, one can easily tell the instar of the occupant if one knows what species is involved. The latter reservation is necessary because the first instar burrow of a large species may be as large as the second or third instar burrow of a small species.

Food and feeding. After the burrow has been dug, the larva assumes a position at the entrance to lie in wait for food. The head and pronotum together form a circular lid or plug to the burrow and are usually colored so that the larva is very well camouflaged. Surprisingly, only one species of larva known from saline habitats, *C. togata*, has a light coloration of these parts of the body. However, some species, *C. nevadica* in this study, *C. silvicola* (Reineck, 1923), and *C. sexguttata*, accumulate a thin layer of soil on the pronotum and thus are even better camouflaged.

In maintaining its position at any point in the burrow, the larva uses its legs and abdomen. The front and hind legs are directed ventrad and the middle legs dorsad. The abdomen assumes a sigmoid position; the first five segments are bent ventrad, giving the larva a swayback appearance; the spines and large setae on the fifth abdominal tergum dig into one burrow wall; the rest of the abdomen is directed forward perpendicular to the axis of the burrow; and the spines on the tenth abdominal segment dig into the opposite burrow wall. Thus the larva is supported at eight points: the six legs and the fifth and tenth abdominal segments. To move down the burrow, the larva straightens its abdomen, flexes its legs, and if the burrow is vertical, falls with the aid of gravity (if the burrow is not vertical, the legs are used); to move up the burrow, the legs alone are used, although Shelford (1911) said that the abdomen assists also. Larvae are easily frightened and will drop down their burrows at the slightest footstep or movement of a human observer.

The larva usually lies in wait at the burrow entrance continually during favorable weather, by night as well as by day. Sometimes however, larvae close their burrows at night, and they frequently do so after feeding. If suitable prey alights or crawls over the burrow, it is very quickly seized by the larva's mandibles. A click is often heard when the prey is seized, apparently caused by the mandibles striking together. Wigglesworth (1929), in experiments on unidentified African species (probably of several genera), said that the larvae will not strike unless certain tactile setae on the back of the head and front of the pronotum are stimulated. Enock (1903), however, stated that the larva of *C. campestris* strikes when the prey is within 1.5 cm. He also gave a good description of how the larva strikes: the larva throws its body backward half out of the burrow; the median hooks of the fifth abdominal tergum dig into the edge of the burrow to anchor the larva. Friederichs (1931) noted the importance of vision in catching prey and said that the larva strikes in the above manner when the prey is between 3 and 6 cm away. Of course, if the prey should land very close to or directly on the head of the larva, it does not strike in the above manner, but simply snaps its mandibles shut on the prey. Probably vision is most important in the day and tactile senses at night for prey capture. The hooks of the fifth abdominal tergum, directed anteriad, serve to help prevent the larva from being pulled out of the burrow by strong prey.

Those species that build pits below the burrow entrance appear to use them as traps. Criddle (1910) and Shelford (1908) reported this for the larva of *C. formosa*; throwing small ants in the pit resulted in their immediate capture, according to Criddle.

The prey, if small enough, is usually dragged down the burrow to be eaten; if it is too large, it is held at the top of the burrow, but large prey items may be taken down the burrow after they have been partially eaten. A third instar larva of *C. circumpicta* that was observed in the laboratory sometimes quickly and sometimes slowly (in one case not for one hour) dragged the prey part way or all the way down the burrow; then it often turned around in the burrow before eating. Sometimes (in the laboratory) a larva, instead of eating the prey, would return to the entrance within a short time and lie in wait again. Two larvae of *C. willistoni* were thus "fed" repeatedly; one dragged 21 adult *Anagasta kuehniella* moths down its burrow, and the other 30, within one hour (three days later the first larva had thrown 13 moths out of its burrow, uneaten, and the other did the same with 15 moths three days after that; other uneaten moths were found when the burrows were dug up a month later after the larvae had died). Such behavior is probably not normal. In eating, the larva manipulates its prey slightly with its mouthparts. Wigglesworth (1929) said that larvae eject fluid (with a pH of 6.2-6.4 and containing trypsin) from the mid-intestine which predigests the prey; the larva then consumes the liquified tissues, straining out solid particles with setae on the labium. The hard cuticular portions of the prey are not eaten and are disposed of, either by tossing them out of the burrow or keeping them in the end of the burrow. The latter method has only been found to be used by *C. silvicola* (Reineck, 1923), *Megacephala brasiliensis* (Zikan, 1929), and *Amblychila cylindriformis* (Williams and Hungerford, 1914). Unacceptable prey is tossed away.

Larvae will eat nearly any small arthropod they can catch. Literature references indicate that food eaten in nature includes caterpillars and other insect larvae, butterflies, moths, flies, beetles, dragonflies, ants, spiders, centipedes, and land crustaceans. In captivity, larvae have been fed houseflies, ants, sowbugs, small beetles, decapitated woodboring larvae, ant pupae, thysanurans, caterpillars, small pieces of raw meat, and apple (it is unlikely that apple was eaten). Criddle (1910) said that larvae of *C. formosa* do not accept Hemiptera. I have only once found a larva eating in nature, a first instar larva of *C. willistoni* that had a salticid spider at the top of its turret. Dr. F. E. Kurczewski (personal commun.) has seen larvae of an unidentified species eat a wasp, *Tachysphex terminatus*. In the laboratory I have fed larvae small spiders and phalangids (a large phalangid was refused), mayflies, nymphal short- and longhorned grasshoppers, nymphal cockroaches *(Supella supellectilium)*, mirids (*Adelphocoris rapidus* and others), nabids, cicadellids (nymphs and adults), an immature fulgorid, aphids, chrysopids, a small cantharid, trichopterans, various caterpillars (including arctiids, geometrids, and a noctuid), small adult moths (including *Anagasta kuehniella*), small adult flies (including a culicid, a syrphid, a bombyliid, a trypetid, a calliphorid, and other muscoid species), and ants. An immature cercopid was not readily accepted. Silphid, coccinellid, and chrysomelid larvae were rejected (one coccinellid larva was manipulated by the larva's mouth-parts for 10-15 seconds, then forcibly flipped out of the burrow unharmed). Sawfly larvae (Tenthredinidae ?) were sometimes refused and sometimes eaten. A small bee was refused by one larva but accepted by another. Goldsmith (1916), Macnamara (1922), Reineck (1923), Schaupp (1879b), and Shelford (1908, 1911) mention that larvae may eat each other in captivity. Some authors attribute cannibalism to crowding and others to hunger. I have noted cannibalism once; a beheaded larva was found outside its burrow in a jar that contained three larvae. Dr. F. E. Kurczewski (personal commun.) has seen on three occasions an unidentified species of larva in Groton, Tompkins County, New York, eating adult *C. formosa*, starting at the abdomen. As will be mentioned later, I once found a *C. circumpicta* with its abdomen missing. We may thus conclude that nearly all small arthropods are acceptable as food to larval *Cicindela*. The time since the last meal probably also affects the acceptability of food, but has not been investigated.

Macnamara (1922) was surprised to find how seldom larvae catch prey in nature; in over ten hours of watching a group of *C. tranquebarica* larvae, he only saw one small ant eaten. He also said that the larvae throw their semi liquid excrement away from the burrow.

The time interval between meals depends on the individual, the instar, the size of the meal, and probably also on the species and temperature. Some larvae in the laboratory ate *Anagasta kuehniella* moths about every other day, while others ate very irregularly and often fasted for a number of weeks. The rough treatment of being caught and transported and the artificial conditions in the laboratory apparently made some larvae refuse to come to the tops of their burrows for food, with the result that they starved to death. In nature, of course, nothing is eaten during estivation or hibernation.

Molting and stadia. First instar larvae only need one meal (if it is large enough) to store enough energy to molt; second and third instar larvae need several meals. As mentioned above, the larva usually closes its burrow while it molts. Shelford (1908) stated that the larvae he studied take about five to seven days to molt; i.e., the burrow is closed that long (as far as is known, no one has seen the actual molting process). Zikan (1929) found that some tropical genera have five instars and close their burrows for two to four weeks during molts. Huie (1915) reported that *C. campestris* larvae closed their burrows about ten days while molting at the start of the second instar. I have

Table 3. Length of stadia in days of larvae reared in the laboratory. Numbers between dots are numbers of days spent between the two events in the respective columns; numbers in parentheses are number of *Anagasta kuehniella* adults (A) or larvae (L) eaten.

Species	First Instar				Second Instar				Third Instar		
	burrow open		burrow closed		burrow open		burrow closed		burrow open		burrow closed
C. circumpicta	●	12	●	102	●	34	●	105	●		
						8(A)					
C. duodecimguttata									●	47	●
C. nevadica					●		26		●		
					●		148		●		
C. togata			●	22	●	29	●	14	●	243	●
						(8A)				(14A)	
					●	68	●	72	●	91	●
						(5A)				(15A, 1L)	
					●	110	●	54	●	62	●
						(7L)				(13A)	
										217	
									●	31	●
										(4A)	
					●	54	●	37	●	52	●
						(7A, 2L)				(9A)	
	●		99		●		39		●		
					●		114		●		
C. willistoni	●		19		●	1?	●	12		193	●
										(13A)	
			●	9	●	17	●				
						(9A)					
						118					
					●	341	●				
						(40A)					
			●	8	●	27	●				
						(5A)					

found that a larva of *C. duodecimguttata* in the laboratory closed its burrow four days to molt from first to second instar, while a *C. willistoni* took seven days to make the same molt (after eating one *Anagasta kuehniella* three days before closing its burrow). These seem to be minimal times; other larvae closed their burrows for many weeks or months, then appeared as the next instar. The enlargement of the burrow to fit the new instar occurs after molting.

The interval between molts (stadium) varies with the individual, the species, the instar, abundance of food, amount of favorable weather, and temperature. Shelford (1908) stated that the first instar larva of *C. limbalis* molts about three to four weeks after hatching; the other stadia are much more variable, the second being about five weeks and the third about ten to eleven months under favorable conditions. Huie (1915) said that the first stadium of *C. campestris* is about six weeks. Zikan (1929) found that the stadia lasted from one to four months, the first being the shortest. Stadium lengths and molting intervals found in this study are shown in Table 3. As can be seen, there is much individual variation, much is probably due to the artificial laboratory conditions. There seems to be much less variation in the amount of food consumed in a stadium than in the length of stadia. The number of moths eaten in normal second stadia ranged from 5-9, and 9-15 for third stadia; the first instar probably can molt after eating one moth. The average weight of an *Anagasta kuehniella* adult is about 0.01 g; thus the amount of whole moths needed for the stadia is: first stadium, 0.01 g; second stadium, 0.05-0.09 g; third stadium, 0.09-0.15 g. Because of the individual variation and the small number of larvae reared in this study, few definite conclusions can be drawn about the lengths of stadia. For *C. togata,* the minimum time for the second stadium under laboratory conditions is about four to five weeks. As will be seen later, hibernation and estivation greatly lengthen the stadia in which they occur.

Activity. Field observations indicate that some larvae of most species are active throughout the warm months (in Kansas, from about March through October). This is partly because of the overlap of generations and long life cycle of cicindelids. If conditions become severe (high temperature or drying out of the soil), estivation usually occurs. As mentioned above, larvae are active day and night, but probably not on cold nights.

Those species that live so near the margins of saline habitats that their burrows are near vegetation or on the side of a bank or hummock probably are able to be active for a longer time than species living on bare flats; the vegetation probably reduces the extremes of temperature and temperature fluctuation found on bare flats. However, there is the possibility that larvae of bare flats compensate for this by digging deeper burrows.

Microhabitats. Many authors have noted that the larvae of one species or another occur only in limited or characteristic areas. Shelford (1911) made a detailed study of *C. limbalis*, *C. tranquebarica*, and *C. sexguttata*, and found that the larvae of these species are found in quite restricted areas characterized by vegetation, exposure, slope, and kind and moisture of soil. In laboratory experiments, he found that the adults choose optimum microhabitats for oviposition (see more complete discussion under the adult). Microhabitats of larvae in this study are shown in Table 4.

TABLE 4. Microhabitats in which larvae have been found. The greater the number of X's the more frequent the occurrence of larvae.

Species	Near water, sand bar	Sloping bank, creek bank	Moist bare salt flats	Dry bare salt flats	Small flats, near margin	Near hummocks, among vegetation
C. circumpicta		XXX			XX	XXX
C. duodecimguttata	XX	XXX				
*C. fulgida**		XX			XX	XXX
C. nevadica		X			XX	XXX
C. togata		X	XXX	XX	XX	XX
C. willistoni			XXX	XX		

* Few larvae have been collected of this species.

As noted above, larvae usually dig their burrows where their eggs were oviposited; however, a number of workers have found that the larvae of some species will leave their burrows if conditions are unsuitable. Shelford (1908, 1911) stated that the larvae of *C. hirticollis* and *C. repanda* often leave their burrows if the soil becomes too dry or too wet; under extreme conditions, such as flooding of the habitat, a small percentage of larvae of the other species he studied left their burrows. Montgomery and Montgomery (1930) also noted larvae of *C. hirticollis* leaving their burrows, and Hefley (1937) saw larvae of *C. cuprascens* moving to a cooler, moister place.

The question of how species of fluvial habitats, whose larvae inhabit sand bars and stream banks, survive flooding is intriguing. Criddle (1907) thought that both larvae and adults of *C. duodecimguttata* must often die in hibernation when their habitat is flooded. Hamilton (1885) noted that hibernating adult *C. repanda* survived flooding for seven days. I have seen active larvae and swarms of adults in areas that had been recently flooded, so cicindelids most certainly do survive flooding. Possibly air trapped in their closed burrows is instrumental in their survival. Floods that cause much erosion probably wash out and kill many beetles.

Larvae can tolerate a certain amount of disturbance of their habitat, such as cattle walking and disfiguring the soil or plowing by man, but cicindelids are generally absent from areas where such disturbance is frequent or prolonged.

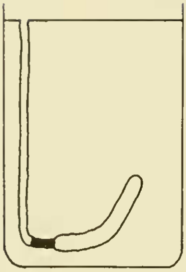
Predators and parasites. Predators of larvae are few; Grandi (1951) stated that histerid beetles of the genus *Saprinus* penetrate larval burrows and eat the occupants; Zikan (1929) said that birds occasionally eat larvae, and that ants *(Solenopsis geminata)* frequently dig into the larval burrow, sting the larva, and eat it; Shelford (1911) reported that ants may overcome a *C. limbalis* larva, and after chewing off its antennae and tarsi, drag it from the burrow. No evidence of predation on larvae was seen in this study.

A number of larval parasites are known. Reineck (1923) reported that *C. silvicola* larvae are occasionally found dead and covered by a moldlike substance; however, he did not mention that the larvae might have died from other causes and their dead bodies later attacked by fungi. Shelford (1913a) studied the life history of a bombyliid fly, *Anthrax analis*, which he found parasitizing *C. scutellaris* and *C. hirticollis*. The adult fly oviposits in larval burrows; the fly larvae attach to the thorax or abdomen of the cicindelid larva and feed from the outside. After the cicindelid larva has built its pupal cell (see next section), the last instar fly larva pupates. The fly pupa digs its way to the surface and the adult emerges. Shelford also said that the larvae of *C. limbalis* were parasitized by a larva somewhat different from *Anthrax analis*. Hamilton (1925) stated that four larvae (out of 34 collected) of *C. obsoleta* (?) were parasitized by a total of seven dipterous larvae, which he assumed to be *Anthrax analis*. Frick (1957) reported that he saw a small black bombyliid (not collected) oviposit in three larval burrows of either *C. haemorrhagica* or *C. pusilla*; the burrows were soon closed by blowing sand, and in a few weeks no larvae could be found. Williams (1916) found some larvae of *C. punctulata* (?) parasitized by orange maggots, probably *Anthrax*. Batra (1965) saw *Anthrax analis* apparently ovipositing in burrows of cicindelid larvae. James K. Lawton *(in litt.)* has found larvae of *C. tranquebarica* in Wisconsin parasitized by *Anthrax analis*; adults were seen ovipositing one to three times in larval burrows. Dr. F. E. Kurczewski (personal commun.) has seen *Anthrax albofasciatus* ovipositing in *Cicindela* larval burrows in New York. I have often seen adults of *Anthrax analis* in saline habitats and once saw one oviposit repeatedly in two burrows of second instar *C. togata* (?) before being collected. The fly lands beside a burrow, stands high on its legs, and bends the tip of its abdomen forward, flipping eggs at the entrance. I have found no parasites on any larvae that I have collected throughout the central United States.

Criddle (1919) stated that the chalcid wasp, *Tetrastichus microrhopalae* (Eulophidae), was reared from *C. limbalis* larvae. Williams (1928) reported that two species of tiphiid wasps of the genus *Pterombrus* (misspelled "*Pterombus*") parasitize larvae of *Cicindela* sp. and *Megacephala affinis* in Brazil. A number of species of the tiphiid genus *Methocha* have been found to parasitize cicindelid larvae: *M. ichneumonides* in Europe (Bouwman, 1909; Champion and Champion, 1914; Champion, 1915; Pagden, 1925; and others), *M. striatella* and *M. punctata* in the Philippines (Williams, 1919), *M. japonica* and *M. yasumatsui* in Japan (Iwata, 1936), *M.* sp. in Brazil (Zikan, 1929), *M. californicus* in California (Bridwell, 1912; Burdick and Wasbauer, 1959), and *M. stygia* in Massachusetts (Williams, 1916) and Wisconsin (James K. Lawton, *in litt.*). The antlike female wasp approaches a burrow with the larva lying in wait at the entrance and induces the larva to seize it (in other cases the wasp avoids the mandibles of the larva). Then the wasp curls its abdomen under the heavily sclerotized head and stings the larva in the tender, membranous neck region, paralyzing it. After secondary stingings, the wasp lays an egg on the venter of the thorax or abdomen. Then the burrow is closed partially or level with the surface by the wasp. The wasp larva feeds from the outside and may change positions. Pupation occurs off the remains of the host. No parasitism by Hymenoptera was noted in saline habitats; however, a *Pterombrus rufiventris* was collected on salt flats in northern Kansas. The life cycle of this species is unknown.

The pupal cell. Before pupation the third instar larva closes its burrow (normally) and digs a chamber for pupation, the pupal cell. The diameter of the pupal cell is about twice that of the larval burrow. It may simply be an enlargement of the larval burrow or adjoin the larval burrow directly (*C. campestris*, Enock, 1903; *C. limbalis*, *C. lepida*, *C. punctulata*, Shelford, 1908). In other species, a tunnel the same diameter as the larval burrow and branching off the latter is built between the pupal cell and the larval burrow (*C. limbata*, Criddle, 1910; *C. scutellaris*, Shelford, 1908). The soil from these new cavities is used to plug much of the larval burrow. The walls of the pupal cell are made smooth by the larva with the mandibles and ventral side of the head. The shape of the pupal cell varies in different species; in some it is only about twice as long as wide and oval; in others it is very elongate and slightly bowed. There is some intraspecific variation in the shape and position of the pupal cell relative to the larval burrow. The pupal cell is built relatively close to the surface, often as close as 2.5 cm. Shelford (1908) found in experiments that the depth of the pupal cell is influenced by soil temperature, being greater the warmer the soil. Some typical pupal cells that I found in laboratory-reared individuals are shown in Figures 68-71.

The Pupa. Having completed construction of the pupal cell, the larva becomes quiescent, head up, with the thorax and abdominal hump resting against the bottom or side of the cell. At the end of one to three weeks, it is not able to move its legs. The abdomen gradually thickens and turns a translucent cream color, indicating internal changes. The tubercles of the first five abdominal segments of the pupa (see below) can be seen through the larval skin folded toward the midline. A few days after these changes, the larval cuticle splits along the frontal suture of the head and the dorsal thoracic midline. Contractions of the ventral muscles flex the body slightly, and the head is gradually withdrawn. The abdomen is freed by later movements. Ecdysis is accomplished in only a few minutes. Just after emergence, the pupa is only slightly shorter than the larva, but it soon contracts to its normal size. The above events have not been seen personally and have been taken from Shelford (1908) and Enock (1903). However, one larva of *C. circumpicta* became quiescent after digging the pupal cell the previous two days;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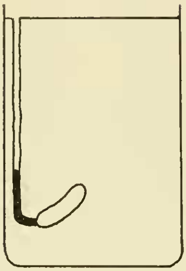
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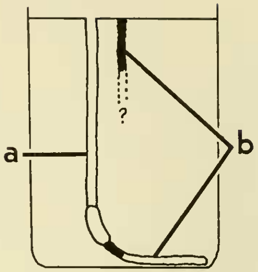

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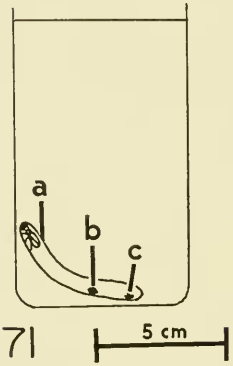

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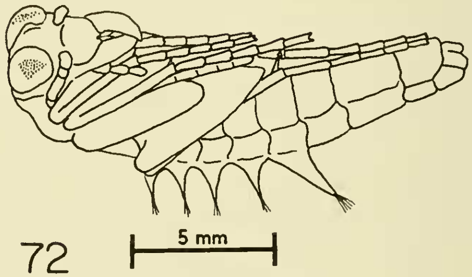

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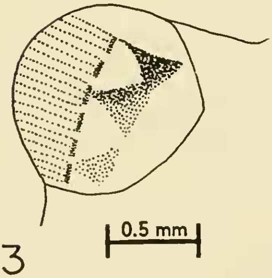

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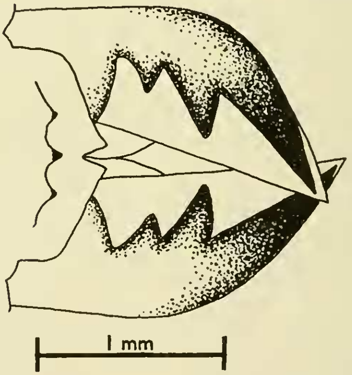

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FIGS. 68-69. Pupal cells and larval burrows (partly plugged) of *C. circumpicta*, from 1 mi. northwest of Fredonia, Wilson Co., Kansas, shown in laboratory rearing jars. FIG. 70. Pupal cell, adult escape burrow (a), and portions of larval burrow (b), partly plugged, of *C. togata*, from 3 mi. west, 2 mi. south of Barnard, Lincoln Co., Kansas, shown in laboratory rearing jar. FIG. 71. Pupal cell with newly emerged adult (a), pupal skin (b), and larval skin (c) of *C. nevadica*, from 11 mi. northeast of Hudson, Stafford Co., Kansas, shown in laboratory rearing jar. FIGS. 72-74, *C. cimcumpicta* pupa; FIG. 72, newly emerged pupa, from 11 mi. northeast of Hudson, Stafford Co., Kansas, ventrolateral aspect; FIG. 73, right eye, caudal aspect; FIG. 74, labrum and mandibles of pupa, from 1 mi. northwest of Fredonia, Wilson Co., Kansas, ventral aspect; pupa is about 18 days old.

the period of quiescence lasted 28 days. A freshly emerged pupa of another individual of the same species was dug up 16 days after the larva was last seen.

The newly emerged pupa of C. *circumpicta* (Fig. 72) is creamy white; the thoracic region is darker yellow, and part of the eyes contains light tan pigment arranged in columns (Fig. 73). The first four abdominal segments bear paired dorsal tubercles, each with an apical ring of setae. Those of the fifth segment are larger. The setae and tubercles function to hold the pupa off the substrate. Shelford (1908) gave a brief summary of pupal color changes in C. *purpurea*: in about ten days the eyes have become completely dark brown; about two days after that, the tips of the mandibles and mandibular teeth begin to darken; the darkening of the mandibles is complete in one to two days; about 13 days after pupation, the tarsal claws begin to darken; and 14 to 15 days after pupation, the proximal portion of the tibiae and the outer margins of the trochanters begin to darken. In 1917, Shelford gave a slightly more detailed schedule for C. *tranquebarica*: initial stages are about the same as for C. *purpurea*; the darkening of the tibiae, which spreads from proximal to distal parts, takes two to three days; about the time that this occurs, the middle of the folded adult hind wings (appear as the tips of the pupal wings) begin to darken; color centers on the last two abdominal segments may develop just before emergence of the adult.

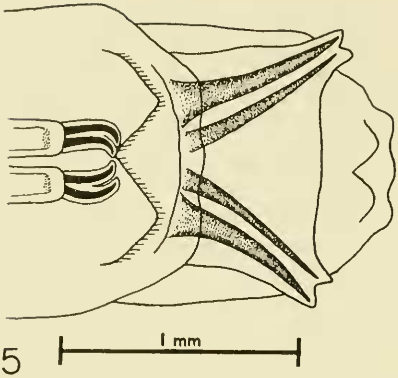
Four pupae of C. *circumpicta*, kept in Stender dishes, were observed during all or part of their development. In the following schedule, the numbers indicate the approximate number of days after emergence:

0-12 or 16: the eye pigment gradually becomes diffused and darker reddish brown until the eyes are uniformly dark brown.

14-18: tips of the labral and mandibular teeth and tarsal claws begin to turn brown (the latter two usually start slightly before the labrum), a process that takes about 1-1.5 days (Fig. 74); soon after this, the apical tibial spines also begin to turn brown.

16-19: a metallic purplish and green iridescence begins to appear on the frons, first antennal segment, and tibiae, later spreading over the head and legs.

17-19: parts of the genitalia begin to turn brown (gonapophyses in ♀ [Fig. 75], aedeagus in ♂), the posterior margin of the eighth abdominal sternum (of ♀) begins to turn brown, the proximal ends of the tibiae and the margins of the trochanters become light brown, and the tips of the pupal hind wings (=middle of folded adult wings) turn light gray; soon after this, spots of light brown appear on the labrum at the bases of the submarginal setae, the apices of the tarsal segments and the tips of the terminal maxillary palp segments become light brown; the terminal few segments of the antennae become light gray, the laciniae of the maxillae become brown, and the clypeal region turns light brown. By now, light brown areas have



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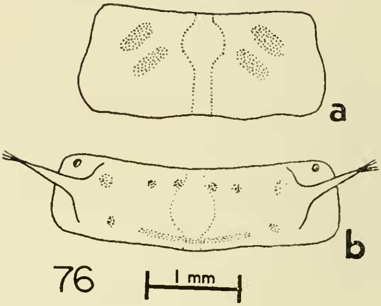

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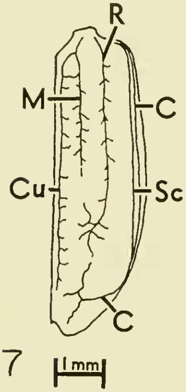

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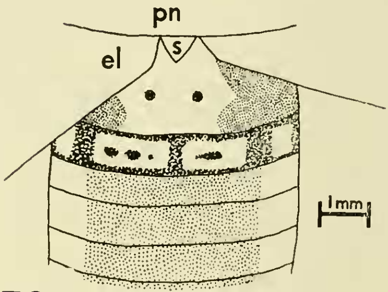

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Figs. 75-76, *C. circumpicta* pupa; Fig. 75, Eighth, ninth, and tenth abdominal segments and apices of hind tarsi of female, ventral aspect; pupa is about 19 days old; Fig. 76, metathoracic (a) and second abdominal (b) terga of same, dorsal aspect; the middorsal position of the heart is shown by dotted lines. Figs. 77-78, *C. circumpicta* adult, from 11 mi. northeast of Hudson, Stafford Co., Kansas; Fig. 77, venation of right elytron (recently emerged), dorsal aspect; C=costa, Sc=subcosta, R=radius, M=media, Cu=cubitus; Fig. 78, mesonotum, metanotum and first three abdominal terga, 15 hours after emergence, dorsal aspect; pn=pronotum, el=elytron, s=scutellum.

appeared on the dorsum of the thorax and abdomen (Fig. 76); the beating heart can easily be seen through the dorsal cuticle, its rate being somewhat variable, with occasional stops, and averaging about 37 beats per minute. The gray of the pupal hind wings spreads to about half their visible surface and becomes darker; about half the tibiae become brown, and the tips of the terminal maxillary palpal segments become dark brown; also the tarsal tips may begin to twitch at or before this point. The gray of the antennae spreads proximad; the pupal skin begins to shrivel. and the dorsal abdominal tubercles become soft.

18-21: the tibiae and tarsi are completely brown (the proximal parts of the tibiae are darkest), and the proximal ends of the femora begin to turn brown. The lateral and posterior margins of the labrum begin to turn brown, the proximal halves of the pupal hind wings begin to turn light gray (the distal halves are very dark gray), the genitalia become darker, and the last three abdominal sternal margins (♀) are light brown. The rest of the maxillary palpal segments become light brown, the bases of the first antennal segments begin to turn brown, the terminal antennal segments are dark gray, and the distal tips of the first, second, and third segments are light brown; the trochanters are dark brown, the distal ends of the coxae and margins of the coxal cavities are brown, and iridescent reflections are visible on all parts of the head and eyes. Movements of the legs, maxillary palps, mandibles, and genitalia may be seen within the pupal skin, and the abdomen may swell and contract slightly. An hour or so later, the movements become more extensive: the head and prothorax are flexed backward; the whole body may be moved slightly (straightened); the mandibles, labrum, maxillary palps, genitalia, and legs are flexed; abdominal movements continue; finally, the legs and maxillary palps are moved freely. The adult may emerge at this point or such movements may continue for several hours. After a flexing of the head and prothorax, the pupal skin is apparently broken dorsally, because several seconds later air bubbles can be seen in the fluid beneath the pupal skin, and the nonbrown portions of the labrum and mandibles, which were translucent, quickly become opaque creamy white. Movements of the abdomen, head, thorax, and appendages assist in extricating the adult from the pupal skin. After about an hour, the head, antennae, front and middle legs, and entire dorsum are free. The body setae are wet and matted. After about two hours the adult has emerged completely. As implied above, the time spent in the pupal stage varies from 18 to 21 or 22 days at a temperature of 24.5°C.

The Adult—*Post Emergence Changes.* Following emergence, hardening and darkening of the adult cuticle is completed. Shelford (1917) described the process in detail for *C. tranquebarica* and less completely for several other species. At the time of emergence, the stage of sclerotization of *C. circumpicta* is more advanced than in *C. tranquebarica* (see description of pupa just before emergence). The newly emerged adult is creamy white except for the above noted parts. The elytra are expanded before the pupal skin is completely off. About 1.5 hours after emergence, the elytral pattern becomes visible because their future pigmented parts have a faint green metallic color. The tracheae of the elytra are easily visible at this time; the typical venation is shown in Figure 77. About 1.5 to 2 hours after emergence, the hind wings are fully expanded and begin to change from translucent to transparent; the veins begin to darken. About 3 to 4 hours after emergence, the distal wing veins are noticeably darker, and about 4 hours after emergence, the hind wings are folded. About 15 hours after emergence the head, prothorax, and femora are light brown, and the elytra are very light brown except where the white pattern will be. The meso- and metanota are creamy white with a few gray spots, and the abdominal dorsum is creamy laterally and dark gray mesally (Fig. 78). The antennal scape and pedicel are brown, the distal ends of the third and fourth antennal segments are brown, and the sixth to eleventh segments are dark gray. In about 3 to 4 hours, the head and prothorax are dark brown and the elytra are brown except the future white pattern, which is translucent creamy white. At about this time, if the individual is a female, the terminal abdominal segments (eighth, ninth, and tenth) begin to retract, a process that is completed about 40 hours after emergence. About 24 hours after emergence, the elytral pattern begins to become more opaque white. About 40 hours after emergence, the beetle can support its own weight and stand. About 68 hours after emergence, the venter of the abdomen is dark, and the antennae, which were held close to the body over the back, are held out in the normal position perpendicular to the long axis of the body. The beetle now becomes quite active, and in nature, adults probably begin digging their way out of the soil at this stage. In captivity, beetles will accept food four to seven days after emergence. About six days after emergence, the elytral pattern becomes opaque white. In the field, adults have been collected with the elytra soft and the pattern still opaque, supporting the conclusion that they dig out of the soil about three days after emergence.

Besides the above changes, a series of color changes, begun in the pupal stage, occurs before the final adult color is acquired. Shelford (1917) studied this in detail, and Huie (1915) noted that on the third day after emergence, *C. campestris* is bluer than when more mature. In *C. circumpicta*, a number of color forms occur, most individuals being either reddish, green, or blue. In the early stages, all individuals show about the same colors: green, blue, and purple on the head, thorax, proximal antennal segments, and legs in the pupal stage and early post-emergence period. In a future green individual, the changes are as follows: from about 4 to 17 hours after emergence, the elytra become almost completely purplish; about 18 to 20 hours after emergence, the head and pronotum, which were purplish, have become brassy green, and the elytra have become purplish and blue; about 40 hours after emergence, the blue of the elytra has increased, a process that continues for over a day; about 70 hours after emergence, the elytra begin to acquire a turquoise color; and about four days later there is more green than blue in the elytral color, but the margins still have a purplish tinge; there is little color change after this. An individual that finally had blue elytra and a green-blue head and pronotum, first had purple-blue elytra and a blue-green

TABLE 5. Percentage of adult *C. f. fulgida* in two color classes (dorsal color) collected at four times of the year in the central United States, and sample size.

Time of coll.	% Bright red	% Purplish red	N
April-early May	72.5	27.5	40
Late May-early June	59.0	41.0	464
Late June-July	20.5	79.5	39
August-September	50.0	50.0	128

Probable scheme of color change in *C. f. fulgida.* The width of the band indicates the abundance of specimens; O=bright red, X=purplish red.

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                O O O O O X X
            O X O O O X O O O X O O X
    O O O O O O O O O O O O X O O X O X X X X
O O O X O O X O O O X O X O O X X O X O X X X X X X X X X X X X X X X
    O O O X O O O O O O O X O O O X O X O X X
            O O X O O X O O X O X O X
                O X O O X X O                           O O
                                                    O O O O O O
                                              O O O O O O X O O O O O
                                                    O O O O O X
                                                        O O

               |                  |                  |
April-ear. May | lt. May-ear. June | lt. June-July     | August-Sept.
```

head and pronotum. An individual that finally had dark cupreous elytra and a brownish head and pronotum was mostly green and cupreous three hours after emergence; the green then increased for about a day, then a reddish wine predominated for about two days before the final color appeared.

As Shelford (1917) noted, individuals of some species continue to change color long after emergence, sometimes until death. I have found that this occurs in *C. fulgida*, at least in its southern subspecies, *C. f. fulgida.* I noticed that most adults collected from northern Kansas in September 1963, and kept in the laboratory over winter were dark purplish red (dorsally) in the spring instead of bright red as they were when captured. When about 270 specimens in my collection and 400 in the Snow Entomological Museum were categorized according to color and time of year collected (Table 5), a trend was noted for most specimens collected in the spring to be bright red and late summer specimens to be dark. A chi square test of independence in a 4 x 2 table was performed on the original data (not %), with the null hypothesis (H_0) being that the time of collection and color are independent. A highly significant X^2 of 27.7 was obtained, rejecting the H_0 and indicating that the color is dependent on the time of collection. Three chi square tests with one degree of freedom were then performed: no significant difference was found between the April-early May and the May-early June groups ($X^2=2.9$); the late June-July and August-September groups were significantly different ($X^2=10.6$); the two early groups combined and the late June-July groups were significantly different ($X^2=21.9$). The bottom of Table 5 shows qualitatively a possible scheme for such data. As will be discussed in more detail later, *C. fulgida* is called "double brooded"; that is, adults emerge from the pupae in the late summer and fall, hibernate, emerge the next spring, and gradually die out in the summer. Freshly emerged individuals are bright red, gradually becoming darker.

The Adult—*Mating.* Many species begin to reproduce soon after emergence as adults, but, as will be discussed later, others hibernate as adults and do not become sexually mature until the spring after they emerge. When sexually mature, and if the weather is suitable, the adults do little else than eat and reproduce. Mating has been observed by a number of workers in the past and seems to be similar in all the genera (Mitchell, 1902, for *Megacephala carolina* and *C. ocellata*;[3] Shelford, 1908, for *C. purpurea*; Moore, 1906, for *C. repanda*; Lengerken, 1916, 1929, for *C. hybrida* and *C. martima*; Goldsmith, 1916, for *C. punctulata*; Fackler, 1918, for *C. cuprascens*, *C. hirticollis*, and *C. repanda*; Zikan, 1929, for *Cicindela*, *Prepusa*, *Euprosopus*, *Iresia*, *Oxychila*, *Odontochila*, and *Megacephala*; Lesne, 1921, for *C. silvicola*; and Pratt, 1939, for *Omus*). I have closely observed mating in the laboratory in *C. circumpicta*, *C. fulgida*, *C. nevadica*, and *C. togata*; and mating pairs of many other species were frequently seen in the field.

The males "take the initiative" and usually approach a female in short runs. When several centimeters away, the male makes a final quick dash and leaps on the dorsum of the female, grasping her between the prothorax and elytra with his mandibles, and frequently around her abdomen with his first and sometimes second pair of legs. Males have a dense brush of setae on the venters of the first four front tarsal segments that are apparently an adaptation for grasping the female. The male supports himself with the last and sometimes second and first pairs of legs (Fig. 79). Males are quite aggressive and have been seen trying to mount other males (specimens pinned on the same pin as "mating pairs" have been seen in museum collections that consisted of two males of the same or different species) or mounted pairs. The female may unseat the male as soon as he mounts and drive him away. If not, the two beetles may remain in the mounted position for some time before or after copulation (a half hour or more), and often the female "goes about her business" of eating, drinking, or ovipositing with a male riding along

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[3] The species which students of American cicindelids have been calling *C. flavopunctata* Chev. should be called *C. ocellata* Klug because the former name is a junior homonym (Schilder, 1953a).

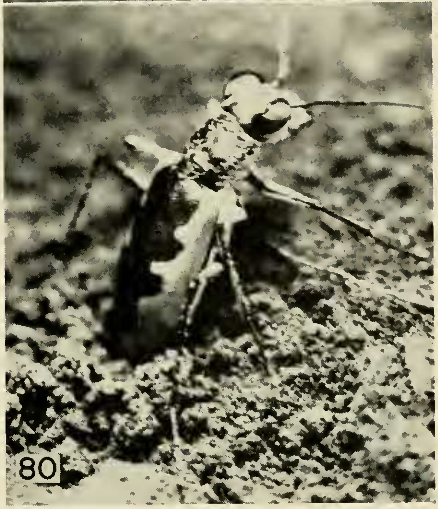


Fig. 79. Mounted pair of *C. togata*, from 3 mi. west, 2 mi. south of Barnard, Lincoln Co., Kansas. Note male's use of mandibles in grasping female. Fig. 80. Ovipositing *C. togata*, from same locality.

(thus, because specimens collected in the field were mounted, this does not mean that they were actually mating). Eventually, the male everts his aedeagus, which normally is retracted within the abdomen, and brings it into a ventral position pointing forward, attempting to insert it into the female's genital opening. The female may make this difficult by turning the end of the abdomen down and may even drive the male away. If the male is successful, the aedeagus is inserted one or several times for one to several minutes each. At this time, the pair may touch and quiver their antennae. Lengerken (1929) said that the male strokes the female's elytra with the palpi of the mouthparts, but I have not seen this. Following couplation, the male may remain mounted or be driven off by the female. Males and females may mate repeatedly with the same or different partners.

The literature mentions mating in the daytime only, and Lengerken (1929) said that it only occurs during hot sunshine; however, I have seen a number of mounted pairs of *C. circumpicta* near Roswell, New Mexico, after dark in the early evening (the soil was still warm from the day). Shelford (1911) mentioned seeing *C. tranquebarica* mating and ovipositing in the laboratory on damp, cloudy days.

The Adult—*Oviposition.* Oviposition has occasionally been seen in nature. Ponselle (1900) mentioned it for *C. flexuosa*; Mitchell (1902) saw it in *Megacephala carolina* and *C. ocellata*; Moore (1906) twice saw *C. repanda* ovipositing; Shelford (1908) reported on *C. purpurea*; Huie (1915) noted that *C. campestris* fills the oviposition hole and may eat its own egg if disturbed during oviposition; Goldsmith (1916) said that *C. punctulata* may oviposit in cracks if the soil is hard; Fackler (1918) briefly commented on *C. repanda*; Lesne (1921) reported on *C. silvicola*; Lengerken (1929) mentioned that eggs are apparently laid singly in the soil; Zikan (1929) said that all the cicindelids he observed close their oviposition holes with material from a second hole made at the same site but slanting obliquely.

I have observed oviposition in the laboratory in *C. circumpicta* and *C. togata.* The ovipositor consists of the eversible terminal abdominal segments (eighth, ninth, and tenth) and the sclerotized gonapaphyses of the eighth and ninth segments, and has been morphologically studied by Shelford (1908), Tanner (1927), and Zikan (1929). In seeking an oviposition site, a female *C. togata* was seen touching her antennae to the soil and occasionally biting the soil with her mandibles. Occasionally, she dug for a short time with her ovipositor. Females often dig holes into which no egg is laid. These have been called "exploratory" or "test" holes, in the literature. When a suitable site has been found, the female digs a true oviposition hole. In digging, the ovipositor is everted and the body is inclined at a steep angle by the front and middle legs (steeper in *C. togata* than in *C. circumpicta*). The hind legs are spread wide for support (Fig. 80). The gonapophyses are the primary digging tools, and the abdomen makes assisting thrusting motions. Sometimes some soil is removed from the hole by an upward motion of the whole body. The oviposition holes takes about five to ten minutes to dig and is from 0.5 to 1 cm deep. The female then remains quiet for several seconds while the egg is laid. Then the hole is usually filled, apparently sometimes with soil from an oblique hole at the same site, as reported by Zikan (1929), and also using the loose soil around the hole that was thrown out in digging. The soil is tamped with the end of the ovipositor, the whole body assisting in the motions, and finally the soil is raked with the gonapophyses, leaving little or no trace of its having been disturbed. The filling of the hole takes one or two minutes; the entire oviposition process usually takes eight to twelve minutes. Occasionally, *C. togata* have been seen not to fill the oviposition hole, and Shelford (1908) said that *C. purpurea* does not close its holes. This would seem to be very harmful to the egg by permitting desiccation. One egg is laid in each hole. I have only once seen a cicindelid oviposit in nature, a *C. circumpicta* near a saline pool near Roswell, New Mexico, on a hot, sunny day.

Shelford (1908) reported watching a *C. purpurea* lay about 50 eggs, and was uncertain as to whether more might be laid. This is the only known estimate of fecundity.

Shelford (1911) did interesting experiments on the selection of the oviposition site, placing adults in cages containing different types of soil and different degrees of slope and moisture. He found that *C. limbalis* chooses only clayey soil and prefers steep slopes; *C. tranquebarica* oviposits in many kinds of soil, but prefers sandy, moist soils; *C. sexguttata* prefers sand with a small amount of humus and usually oviposits near or under twigs or leaves. He also noted that oviposition sites are different from or more restricted than the habitats in which the adults hunt for food. Thus it seems that the adults select optimal microhabitats for the larvae.

The Adult—*Food and feeding.* There have been many notes in the literature concerning the food of adult cicindelids; those for the genus *Cicindela* are summarized in Table 6. In addition, past workers have fed the following to adults in captivity: decapitated woodboring beetle larvae, mealworms (*Tenebrio* larvae), caterpillars, a tipulid fly, a large tabanid fly, calliphorid larvae and adults, freshly killed house flies, and ants. Arthropods that I have seen eaten or attacked by *Cicindela* in the field and in the laboratory are listed in Table 7. From these lists, one may conclude that adults of *Cicindela* eat nearly any arthropod that they can subdue and which occurs in their microhabitat. Occasionally, a beetle will reject an insect that possibly may possess distasteful chemicals, but at other times such insects are eaten. Probably the degree of hunger of the predator affects the acceptability of distasteful prey.

Balduf (1925) observed a *C. punctulata* catch and eat nine large nymphs and one adult chinch bug, *Blissus leucopterus*, in 26 minutes. The beetle saw the bugs from 5 to 8 cm away (in all cases they were moving), and after catching them in its mandibles, struck them against the ground several times in rapid succession before eating them. The beetle returned to a certain elevated spot to eat; the exoskelton of the prey was discarded in the form of a small pellet. Lesne (1921) also noted that the hard parts of the prey are discarded. Moore (1906) noted that *C. purpurea* may return to its adult burrow to eat its prey, that it could seen ants 10 to 13 cm away, and that it rushed up to an ant, bit it once, and gave it a toss, repeating this behavior until the ant showed no signs of life. He also noted that the vision of *C.*

TABLE 6. Food of *Cicindela* eaten in nature that has been reported in the literature.

- Crustacea—fiddler crabs (young) and marine "fleas" *(C. ocellata)*
- Arachnida—unidentified species of spiders *(C. repanda, C. sexguttata)*
- Insecta
  - Orthoptera
    - Acrididae—*Melanoplus spretus (C. circumpicta, C. formosa, C. fulgida, C. purchra, C. punctulata, C. scutellaris, C. sexguttata, C. tranquebarica); Stenobothrus* sp. (nymph) *(C. silvicola)*
  - Dermaptera—*(C. campestris)*
  - Hemiptera
    - Lygaeidae—*Blissus leucopterus (C. punctulata)*
    - Coreidae—*Leptocoris trivittatus (C. splendida)*
  - Homoptera
    - Aphididae—*(C. tranquebarica)*
  - Coleoptera
    - Carabidae—*Harpalus pennsylvanicus* (*C. sexguttata,* was larger than cicindelid and escaped); *Bembidion* sp. *(C. cuprascens, C. hirticollis)*
    - Heteroceridae—*(C. cuprascens, C. hirticollis)*
    - Elateridae—*Horistonotus uhleri (C. rufiventris)*
    - Coccinellidae—*(C. hybrida)*
    - Tenebrionidae—*Tenebrio molitor (C. hybrida)*
    - Chrysomelidae—*Disonycha quinquevittata (C. formosa)* *Leptinotarsa decimlineata* (small larvae) *(C. punctulata)*
    - Curculionidae—*Phytonomus punctatus ? (C. repanda ?)*
    - Small, unidentified adults—*(C. tranquebarica)*
  - Lepidoptera
    - Phalaenidae—*Pseudalctia unipuncta ? (C. sexguttata)*; unidentified larvae ("cutworms") *(C. scutellaris, C. tranquebarica)*
    - Notodontidae—"puss moth" *(C. campestris)*
    - Galleriidae—*Galleria melonella* (larva) *(C. hybrida)*
    - Pieridae—"white butterfly" *(C. campestris)*
    - Unidentified larvae *(C. campestris)*
  - Diptera
    - Calliphoridae—*Lucilia caesar (C. hybrida); Calliphora volitoria (C. hybrida)*
    - Sarcophagidae—*Sarcophaga camaea (C. hybrida)*
    - Unidentified muscoid larvae and adults *(C. repanda)*
    - "Gnats" *(C. sexguttata)*
    - Unidentified larvae *(C. cuprascens, C. hirticollis)*
  - Hymenoptera
    - Formicidae—*Pogonomyrmex occidentalis (C. fulgida); Formica pallidefulva (C. formosa,* was unsuccessful); unidentified adults *(C. ocellata, C. formosa, C. longilabris, C. punctulata, C. purpurea, C. repanda, C. scutellaris, C. sexguttata, C. tranquebarica)*
    - "Bees"—*(C. tranquebarica)*
    - Halictidae—*Lasioglossum zephyrum* (dead adults) *(C. repanda); Nomia melanderi* (dead adults) *(C. haemorrhagica, C. pusilla)*
- Other
  - Freshly dead carcasses (fish, rabbits, etc.) (*C. ocellata*—this is doubtful; perhaps they were eating carcass-feeding insects)

TABLE 7. Arthropods that adults of *Cicindela* have eaten or attacked in the field (F) and in a laboratory terrarium.

- Arachnida
  - Salticidae (F)
  - Lycosidae ?
  - Small, unidentified species
- Insecta
  - Orthoptera
    - Gryllidae—*Oecantha* sp. (nymph)
    - Tettigoniidae—(nymph over 1 cm long)
  - Hemiptera
    - Gelastocoridae—*Gelastocoris* sp. (F) (attacked, but not eaten)
    - Miridae
    - Nabidae—*Nabis ferus*
    - Lygaeidae—*Ischnoderus falicus*; nymph of another species
    - Cydnidae (F)
    - Pentatomidae (nymph)
  - Homoptera
    - Cicadellidae
    - Aphididae (F)
  - Neuroptera
    - Chrysopidae
  - Coleoptera
    - Cicindelidae—*Cicindela togata*
    - Caradibae—*Anisodactylus* sp. (F)
    - Coccinellidae (could not get a grip on it, unsuccessful)
    - Chrysomelidae—*Ceratoma trifurcata* (F—unsuccessful, apparently distasteful); *Diabrotica undecimpunctata*; Halticinae (unident.); *Monoxia puncticollis* (F—unsuccessful, apparently distasteful)
  - Lepidoptera
    - Pyralidae—*Anagasta kuehniella*
    - Geometridae (larvae)
    - Small, unidentified caterpillars
  - Diptera
    - Stratiomyidae
    - Tachinidae
    - Muscidae
  - Hymenoptera
    - Formicidae—*Pogonomyrmex occidentalis* (F—ant heads found with mandibles clamped on cicindelid antennae or palps); *Crematogaster* sp. (dealate queen) (F)

repanda seems to be limited to 8 to 13 cm, that it takes *C. repanda* four or five minutes to eat a housefly, and that this species seems to be afraid of ants. Huie (1915) reported that a *C. campestris* in captivity ate freshly emerged adults of the same species. Goldsmith (1916) observed that *C. sexguttata* would give up an attack if the prey offered any resistance. He also watched a group of 27 *C. repanda* feeding on a colony of "small red ants." Another time he saw two beetles of the same species devour a whole colony of ants by alternating eating each ant that came to the entrance of the hole; when no more ants appeared, one beetle dug half the length of its body into the mound in search of more food. Swiecimski (1957) studied the role of sight and memory in food capture by *C. hybrida* in terraria, using various types of live and dead insect bait. He found that the beetles obtain food by random search (only immobile prey) or deliberate attack caused by perception from a distance (up to 25 cm); they do not react to dead prey moved artificially, or are frightened. In random search, vision does not play an important part, the beetle often trying to eat pebbles or other inanimate objects. Apparently chemoreceptors do not function until the prey is very close. Naturally moving prey evokes attack, which may be divided into several stages: 1) preparatory attitude, consisting of elevating the front of the body and turning toward the prey, 2) actual attack, consisting of a quick, interrupted run toward the prey, 3) capture, 4) eating the prey. In some cases, certain stages are omitted, usually caused by variations in the behavior or nature of the prey. Memory of the shape and location of the prey appears to play a part occasionally, because when prey was taken from the beetles, they searched the area where it was, or if it was moved, they reattacked it.

Friederichs (1931) found that European species *(C. campestris, C. hybrida, C. silvicola, C. silvatica)* have binocular vision for about 90° of their forward field of vision, and that they react only to movement. This is probably why beetles turn toward their prey before attacking it : to locate it more accurately.

Evans (1965) gave a detailed account of how the food is eaten by *C. hybrida*. The prey is seized with the long distal teeth of the mandibles; pieces of the cuticle may be cut away to reach the soft inner parts. The food is then raked back into the preoral cavity by rotary movements of the laciniae and accumulates in the form of a bolus that may be chewed for some time by the proximal molar portions of the mandibles. The maxillae move only slightly and, together with the labial palps, help to hold the bolus in place. When enough food is accumulated, the mandibles begin to move the food in a rotary motion in the preoral chamber from the mandibles upward and backward, across the cibarial opening, and down between the labial palps. The labial palps may then push the food up to the maxillae to be recirculated. Rows of setae on the hypopharynx and epipharynx strain out solid particles and allow only fluid and very small solid particles to enter the cibarium. Evans found some evidence of extraoral digestion, that is, regurgitation of enzymes from the gut. Lengerken (1929) also supposed that this occurs.

Observations that I have made on the feeding behavior of *C. circumpicta*, *C. duodecimguttata*, *C. fulgida*, *C. nevadica*, and *C. togata* in the laboratory confirm many of the above reports. *C. togata* saw the movements of small spiders (about 2 mm long) from a distance of 2 to 8 cm, and *C. fulgida* saw adult mites *(Androlaelaps casalis)* about 1 mm in diameter from 2 to 3 cm away (the mites are scavengers that probably were carried into the laboratory with the soil). The prey, if it is distant, is approached by a series of short runs; the beetle then lunges at it with the mandibles open. If the prey is small or stops moving, the beetle may miss it and lunge repeatedly, often merely biting the soil. The beetle seems to rely almost entirely on sight; if the prey eludes it in the above manner, the beetle searches "blindly" the immediate area and does not recognize immobile prey until its head is almost directly over it. Once the prey is seized with the distal part of the mandibles, the beetle may become quite excited, running about, holding the prey with its mandibles. Its excitement is often transferred to other beetles in the terrarium, which also run about searching for food or fighting with the successful individual for the prey. Usually the prey is first masticated thoroughly with the distal parts of the mandibles and maxillae. These organs move laterally alternately and gradually work the prey back and forth. This operation takes about two minutes for a small catepillar about 5 mm long and probably serves to break up large sclerites of the prey. Then the food is moved farther back into the preoral cavity for mastication and circulation as described by Evans (1965). This process may take five to ten minutes, and is occasionally interrupted by the mouthparts becoming still and the head and prothorax being protruded slightly. This is interpreted as swallowing. During mastication, the mandibles are moved laterally quite regularly and mechanically at a rate of 80 to 140 times per minute. Finally, a small, compact pellet about 1 mm in diameter is ejected and laid on the substrate by the beetle. After a beetle had eaten an *Anagasta kuehniella* caterpillar, the resulting pellet was put into water and teased apart. It contained the caterpillar's mandibles, masticated head capsule (broken into irregular pieces ranging from 0.05 to 0.25 mm in diameter), and the thin skin, relatively intact and including setae and proleg crotchets. A medium sized prey (about 5 to 8 mm long) takes about five to 20 minutes to eat. Once a *C. togata* was observed to lay down part of a hemipteran, chew on the other part, then pick up and eat the first part. As noted in Table 7, cannibalism occasionally occurred. One *C. togata* was found without a head, the elytra of another was found, and a third was seen being eaten by an individual of the same species. Probably only weak or sick individuals are cannibalized. In captivity, adults will eat an insect the size of *Anagasta kuehniella* once every one, two, or three days.

Defecation consists of deposition on the substrate of a drop of opaque, pinkish or brownish fluid, which eventually dries into a spot of the same color.

The Adult—*Drinking.* A number of workers have reported tiger beetles drinking in captivity: Moore (1906), Williams and Hungerford (1914), Huie (1915), Lengerken (1929), and Zikan (1929). Apparently only Mitchell (1902) has seen drinking in nature.

I have occasionally seen *C. duodecimguttata*, *C. fulgida* and *C. togata* drink in the laboratory. Moore (1906) reported that although he provided *C. repanda* with a drinking container, the beetles did not use it, drinking instead from moist sand. My beetles drank both from a Stender dish and from moist soil. In drinking, the mouthparts, mandibles agape, or much of the head is thrust into the water or moist soil for one-half to several minutes. Sometimes soil is bitten to bring the moist soil closer to the mouth. Presumably the water is sucked up by the foregut.

Balduf (1935) thought that cicindelids require water as often as food; however, cicindelids have been seen drinking in nature so infrequently that this is questionable. Probably much water is obtained from the food, and many species frequent the moister parts of their habitats, which probably reduces their rate of water loss.

Mitchell (1902) stated that *C. ocellata* eats algae and fine moss near springs, but it is more likely that the beetles were sucking water from these plants.

The Adult—*Burrows and digging.* Many species dig burrows as adults for various purposes. Some hibernate as adults, usually in deep burrows (5-122 cm deep in Canada; Criddle, 1907). During the warm part of the year, many species make shallower burrows in which to spend the night (Davis, 1921; Rau, 1938), and hot or dry weather (Wallis, 1961). Reineck (1923) rainy or cloudy weather (Moore, 1906; Wille and Michener, 1962; Blanchard, 1921; Dengerken, 1916, 1929; Moore, 1906; Mitchell, 1902; Blanchard, 1921), stated that *C. silvicola* does not dig adult burrows, hiding in natural crevices in cold or rainy weather. I have noted, as has Graves (1963), that *C. sexguttata* may take shelter under loose bark. Mitchell (1902) reported that only females of *Megacephala carolina* dig burrows to spend the day (this species is nocturnal), while males hide under logs, trash piles, dead leaves, or bunches of grass. Usually, however, both sexes burrow. Good descriptions of the digging process are given by Moore (1906), Criddle (1907), and Lengerken (1929).

I have noted adult burrows in the field for *C. circumpicta*, *C. duodecimguttata*, *C. fulgida*, *C. hirticollis*, *C. nevadica*, *C. repanda*, and *C. willistoni*, and have made more detailed observations of digging by *C. fulgida* in the laboratory.

In digging, the beetle loosens bits of soil with its mandibles; the soil is then kicked backward under the body by the first, middle, and hind pairs of legs in succession. Soon a pile of loose soil accumulates at the entrance of the burrow, often plugging it. As the beetle goes deeper, it accumulates a small pile of soil directly behind it, then backs up the burrow to push it out the entrance. The beetle may stop occasionally to rest. Most of the burrow is slightly larger than the body width, but the end is larger, to allow the beetle to turn around (it rests facing outward). The entrance is oval and rather ragged in contrast to the round, smooth holes of most larvae. For short stays, the burrow is usually plugged loosely or with a thin plug; hibernation burrows are entirely plugged except for the bottom 10 to 25 cm (Criddle, 1907). The speed of digging depends on the type of soil. In sand, a beetle can dig its body length in a minute (Lengerken, 1929). A *C. fulgida* dug 3 cm in moderately compact clay in one hour. Usually non-hibernation burrows slant gently downward, are more or less straight, and range from 2 to 10 cm deep. Hibernation burrows are more nearly vertical and often crooked, and when in hard soil are shallower than those of the same species in soft soil (Criddle, 1907). In warmer areas, hibernation burrows are not as deep as reported by Criddle; Blaisdell (1912) found 64 *C. senilis* hibernating under three rocks in relatively short, often interconnected burrows. From one to five individuals were in each chamber. More than one individual in the same burrow is uncommon. Criddle (1907) found both *C. duodecimguttata* and *C. tranquebarica* occasionally in the same burrow as *C. repanda*. Moore (1906) sometimes found two or more *C. repanda* in the same burrow. In digging 67 *C. willistoni* from temporary burrows about 3-5 cm long, I found two beetles in the same burrow in only three cases. The burrows were usually plugged except for the bottom 2 cm and had a mound of loose soil over the hole.

C. togata was never seen to burrow in captivity or in the field, although one once spent the night in a *C. fulgida* burrow. They readily take shelter under available objects. Their long legs do not seem to be well adapted for digging.

The Adult—*Cleaning*. Adults frequently clean themselves, as after digging, eating, or drinking. Lengerken (1929) stated that beetles often stop in the midst of digging to clean themselves of sand, and then continue. The front tarsi are rubbed over the front and upper surfaces of the head (simultaneously or one at a time), and the antennae are pulled between the apical tibial spurs and the tarsi of the front legs. The front legs are used to clean the mouthparts and the mouthparts to clean the front legs. Primarily the middle tibiae are used to clean the elytra, although the hind tibiae sometimes assist, by being rubbed quickly over the dorsum. In addition, the distal parts of the legs are cleaned by being rubbed together, two at a time, the first with the middle or the hind with the middle. The front and particularly the middle tibiae bear on their inner apical portions, areas of short, closely set setae that seem to serve for cleaning. When an apparently distasteful insect is seized, a beetle will often dig its mandibles into the soil repeatedly, probably in an attempt to clean them of the offensive substance.

THE ADULT—*Sleep*. Behavior resembling sleep is known in many insects. No specific mention of sleep in cicindelids is known, although some authors implied that sleep occurs in the burrow or other retreat (Rau, 1938; Davis, 1921; Moore, 1906). In the laboratory, I have on several occasions found adults apparently asleep (*C. fulgida*, *C. nevadica*, and *C. togata*). The beetles were motionless in a normal standing position or with the venter resting on the substrate and acted half dead when touched. After several seconds of being prodded, they seemed to "wake up" and became active.

THE ADULT—*Activity*. Many workers have noted that *Cicindela* tends to be most active on hot, sunny days. Lengerken (1916, 1929) and Shelford (1908) noted that mating occurs only in such conditions (see above section on mating). Reineck (1923), Moore (1906), Huie (1915), and others have noted that beetles remain hidden or in burrows on cool and cloudy or rainy days. Lengerken (1916) reported that even a cloud passing before the sun curtailed the activity of *C. maritima* and *C. hybrida*. Davis (1921) watched a *C. tranquebarica* dig at about 4:45 PM a burrow in which to spend the night. Moore (1906) said that *C. repanda* retires at about 5 PM on ordinary days and about 7 PM if the weather is very warm, and that *C. purpurea* remained active until late in the evening if the day was hot. He also said that *C. repanda* becomes active at about 8 or 9 AM or earlier on very warm days. Remmert (1960) found that *C. campestris* alternates variable periods of rest and activity during the day; hungry individuals have longer periods of activity and shorter periods of rest (and vice versa for full individuals); at higher temperatures or in stronger light, the periods of rest are shorter.

I have noted that on hot days, *Cicindela* is active in spite of clouds; in fact, if the habitat is very hot, activity decreases, the bettles remaining in the shade of vegetation or other objects, or in cracks until clouds come and lower the temperature. More will be said about the effects of physical conditions on activity in a later section.

THE ADULT—*Fighting*. Huie (1915) noticed that female *C. campestris* in captivity were frequently disturbed by other beetles running into them, pulling their legs, or seizing them by the body (probably mating attempts). Lengerken (1916, 1929) often noted fighting among captive beetles. Sometimes when two individuals met they would stop and elevate the front of their bodies, mandibles open wide; often this apparent threatening behavior averted actual combat. If two individuals ran into one another from opposite directions, they tumbled around together briefly before continuing on their way. Moore (1906) observed fighting in captive and free *C. repanda*. One beetle rushed at another, snapping at it with its mandibles or merely bumping into it and then running away. The other beetle then chased the first for a while. Legs and antennae were sometimes lost as a result of these encounters in captive individuals.

I frequently observed fighting in captive *C. togata* and *C. fulgida*, often for food. Once two *C. fulgida* were seen fighting for a small lycosid spider, one riding on the others back, both chewing on the spider. Another time a female *C. togata* rushed up to a male that had just caught a small spider; they faced one another and fought with their mandibles for about ten seconds; then the female rushed at the male twice before giving up. In the spring when mating occurs, *C. fulgida* are quite aggressive; one often seized another's leg, and they tumbled around for a few seconds. Once a *C. togata* that was in a *C. fulgida* burrow was quickly approached by a *C. fulgida*; they fought briefly with their mandibles, and the *C. togata* remained in the burrow. A *C. nevadica* was found with a broken left hind tibia that it apparently received in a fight, and specimens with tarsi or antennae missing have been seen. In the field, I once saw a number of *C. circumpicta* rushing at one another in the manner described by Moore (1906).

The Adult—*Flying and escape.* Davis (1921) watched a *C. tranquebarica* for an hour and saw it fly only once; and Moore (1906) watched a *C. purpurea* traverse about 40 meters of a road in an hour without flying. These notes confirm the impression that I have received from casual observations that although most species of *Cicindela* have the power of flight, they rarely fly. When going about their usualy activity of preying, *Cicindela* typically runs in short bursts, often in a zig zag course. Usually only when disturbed by a larger animal do they fly, and even then some species (or under certain conditions) fly only as a last resort.

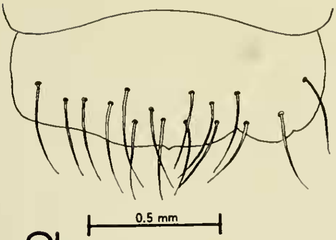
As Moore (1906) noted, before flying, a beetle squats close to the ground. If further frightened, the beetle jumps into the air and takes wing (Moore remarked that deformed beetles unable to fly could jump about 3 cm high). Several authors have noticed differences in the flying abilities and habits of different species. Most species of *Cicindela* fly in a low (1 to 2 m), level path and land 5 to 15 meters from the source of disturbance. Some early authors thought that beetles always landed facing the source of danger, but later observations showed that they land facing the wind (Moore, 1906). Often a beetle will circle and land behind the disturbance, particularly if flushed repeatedly. More intricate midflight maneuvers may be made, if the beetle "sees" it is about to land in unsuitable territory, to bring it to a "desired" landing place.

As implied above, escape behavior varies with the species, the external conditions, and the degree of danger. Moore (1906) noted that *C. purpurea* usually flew only a short distance down a road unless persistently pursued; then they flew into the nearby grass, ran to a clear space, and either flew again or squatted ready to fly. *C. togata*, a species with long legs, often tries to outrun the danger. If hard pressed, it usually runs in a zig zag course and may run into short, sparse *Distichlis* grass rather than fly. When it does fly, it frequently flies into dense grass. The same zig zag running behavior has also been noticed in *C. circumpicta*, and this species was also seen to fly or run into vegetation to escape. *C. fulgida*, which is normally found among sparse vegetation, usually flies at the slightest danger, often into dense vegetation, but sometimes out onto a bare salt flat. Sometimes species that are surprised in short vegetation have difficulty flying because of bumping into the plants. *C. hirticollis* is another very wary species that is difficult to capture. String wind and low temperature generally deter or inhibit flying.

THE ADULT—*Injuries and deformities*. As mentioned above, injuries are sometimes inflicted by other cicindelids. Townsend (1884) mentioned finding *C. tranquebarica* with antennae, legs, or elytra injured or missing. I have collected specimens with injuries that probably were not caused by fighting. A *C. fulgida* was collected with both hind tibiae and tarsi missing, a *C. togata* was found with the tip of one elytron missing, and a *C. circumpicta* was found on its back, legs kicking, with its entire abdomen missing. Probably predators inflicted these injuries.

Several authors have reported deformities in cicindelids. Moore (1906) noted that some *C. purpurea* have fused elytra and cannot fly. Townsend (1884) found a *C. tranquebarica* with a wrinkle across one elytron and noted (as I have) that some individuals of this species cannot fly. Horn (1927) reported atypical elytral markings, short elytra, deformed leg segments, and a deformed head and prothorax in *Cicindela* and several other genera. Shelford (1913c) showed atypical patterns of elytral tracheation in *Cicindela*. Shelford (1915) noted that leg and antennal abnormalities are rare, while elytral and labral abnormalities are more common in nature. He also experimentally produced deformities by injuring larvae and pupae of *C. punctulata*; injuring the pupal labrum produced adult deformities, but injuries to the pupal legs or larval labrum had little or no effect on the adult. He thought that elytral deformities such as an abnormally short elytron (often accompanied by reduced markings) or holes in the elytron were caused by injuries to the pupal elytra. I have occasionally found labral and elytral deformities in *Cicindela*; some of these are shown in Figures 81-84.

Wood (1965) found a *C. scutellaris* with a trifurcate ninth antennal segment (each fork having two additional segments), and noted that similar abnormalities have been reported in a cerambycid. Park (1931) and Lavigne (1965) found them in a tenebrionid and cerambycids. I collected a *C. nevadica* with a similar deformity, Figures 85 and 86. The third segment of the left antenna is bifurcate at the apex, and segments four to eleven are duplicated.



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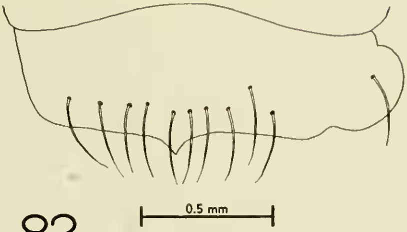

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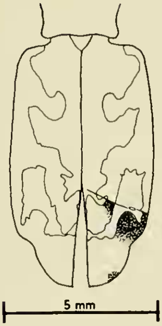

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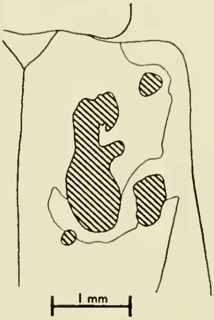

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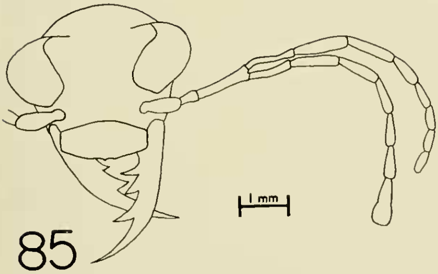

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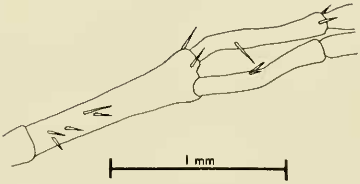

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FIG. 81. Deformed labrum of male *C. nevadica nevadica*, from Saltdale, Kern Co., California, frontal aspect. FIG. 82. Deformed labrum of male *C. nevadica knausi*, from 2.5 mi. southwest of Plainview, Woods Co., Oklahoma, frontal aspect. FIG. 83. Normal (left) and deformed (right) elytra of female *C. nevadica olmosa* (paratype), from 25 mi. west of Tularosa, Sierra Co., New Mexico, dorsal aspect; a crease runs transversely across the right elytron, interrupted by a small hole near the margin; stippled areas are discolored (light brown), normally white maculation. FIG. 84. Anterior half of right elytron of female *C. nevadica knausi*, from 1 mi. northeast of Tucumcari, Quay Co., New Mexico, dorsal aspect; shaded areas represent holes; the posterior portion of the humeral lunule (caudad from largest hole) is atypical (see Fig. 83 for typical humeral lunule). FIG. 85. Head and deformed left antenna of male *C. nevadica knausi*, from 3 mi. east of Cherokee, Alfalfa Co., Oklahoma, cephalic aspect. FIG. 86. Enlargement of third and duplicated fourth segments of same.

THE ADULT—*Odor.* It has often been mentioned in the literature (e.g., Leng, 1902; Eckhoff, 1939; Graves, 1963) that *C. punctulata* emits a fruity or applelike odor when handled. Leng (1902) also reported that *C. sexguttata* emits a fragrant odor and *C. longilabris* a musky odor when captured. Lengerken (1929) noted a pleasant odor produced by *C. maritima* in hot weather and when the beetles were alarmed, as when captured. I have noticed that *C. ocellata* and *C. tranquebarica*, when handled, emit an odor similar to that of *C. punctulata*, but weaker, and that *C. duodecimguttata* produces a musky odor.

These odors are produced by the anal, or pygidial glands. Dierckx (1899, 1901) discussed the anatomy of these glands in *C. hybrida* and *C. campestris*, noting that they are similar to those of carabids, with an oval, cuticular, sparsely muscled reservoir; a collecting canal; and a long, cylindrical gland proper. Brandt (1888) remarked that the anal glands of cicindelids (no species given) are more poorly developed than in carabids because the cicindelids have other well developed means of escape (running, flying) and defense (mandibles). Although the subject has not been studied further, Brandt's explanation is probably correct.

The Adult—*Sound production.* Certain cicindelid genera, *Mantica*, *Mantichora*, *Oxychila*, and *Chiloxia*, possess stridulatory organs, ridges on the margins of the elytra and hind tibiae (Horn, 1908-15). I have noticed that captive *Cicindela (C. fulgida, C. nevadica)* sometimes raise their elytra synchronously very slightly once or several times. Sometimes when this is done, faint but clearly audible sounds are produced, best described as short buzzes. Captive *C. repanda* have been heard making a continuous buzz lasting about one second while the elytra were raised slightly. Apparently the sound is produced by slight irregularities on the elytra where they join, although none are readily visible under magnifications of about 80X. The sound is probably purely accidental.

Sound is also produced in flying species when the wings beat. It is usually not audible to humans except in the larger species, in which a low buzz can be heard as the beetle takes off.

The Adult—*Predators and parasites.* Relatively few records of enemies of adult cicindelids have appeared in the literature. Ingram (1934) found a mite (unidentified) parasitic on the thorax and legs of *C. haemorrhagica.* Graves (1962) watched a dragonfly, *Aeshna interrupta*, catch a *C. repanda* in flight and carry it away. Asilid flies seem to be the most common predator: Fox (1910) reported them catching and eating *C. dorsalis*; Fackler (1918) saw a *Proctacanthus* (near *rufus*) catch a *C. repanda*, inserting the proboscis between the elytra to feed; Bromley (1914) saw *Proctacanthus philadelphicus* eat *C. punctulata*, on three different occasions, and once saw *Promachus fitchi* catch the same species; Davis (1910) saw a *C. sexguttata* caught and eaten by a *Laphria* sp., about as large as the beetle; Wallis (1913, 1961) reported *Proctacanthus milberti* catching a *C. purpurea* and inserting the proboscis between the elytra to feed, as well as asilids twice catching beetles in flight; Stevenin (1948) saw an asilid repeatedly attack a *C. apiata* in Uruguay.

Blaisdell (1912) found evidence that lizards eat *C. senilis*. Zikan (1929) said that chickens and a "wren" may eat adults. Fackler (1918) reported that the remains of *Amblychila* had been found in a hawk's stomach; Fitch (1963) found remains of *Cicindela* in pellets of the Mississippi kite. Criddle (1907) said that badgers sometimes destroy large numbers of adults; Snow (1877) found a freshly eaten *Amblychila* in the stomach of a skunk; Stains (1956) reported fragments of *Cicindela* in scats of the raccoon.

Many of the *C. circumpicta* I collected on 28 August 1963 from near Drummond, Garfield County, Oklahoma, were heavily infested with larval mites of an undescribed species of *Eutrombidium* (Trombidiidae). Most of the mites were under the elytra, on top of the abdomen, and on the hind wings; a few were on the venter of the abdomen. The infestation was apparently only "accidental" because these mites have not been found on the same species from that locality in later years, nor from beetles from other localities. This genus of mites lives in the soil as nymphs and adults, eating orthopteran eggs; larvae have been found parasitizing several genera of orthopterans (Evans et al., 1961). I have also found a number of mites (Uropodidae) attached to the thorax and legs of two museum specimens of *C. sexguttata*. This family of mites is not actually parasitic, but phoretic, attaching to insects in the deutonymph stage for transportation (Evans et al., 1961).

I have twice caught asilids eating *Cicindela*: *Diogmites symmachus* with a *C. togata*, and *Proctacanthus milberti* with a *C. formosa*. Asilids are often common in and near saline habitats.

On a small salt flat in north central Kansas, I found two regurgitated pellets about 1 cm in diameter, which an ornithologist, Dr. Richard J. Johnston, thought were produced by a sparrow hawk. They contained remains of insects: a bee, a carabid, several chrysomelids, and three species of cicindelids, *C. circumpicta*, *C. togata*, and *C. punctulata*. Other birds which eat insects, such as killdeers and snowy plovers, are often common in saline habitats and likely eat some *Cicindela*.

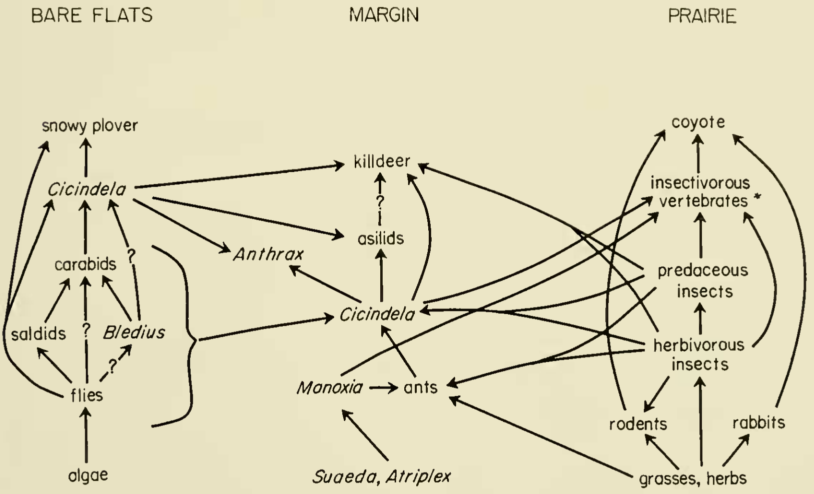
THE ADULT—*Ecological relationships.* Certain of the relationships of cicindelids with other animals have been discussed in the sections on food and predators and parasites. Other arthropods, besides *Cicindela*, that I have seen or collected in saline habitats are listed in Table 8. These relationships can be summarized in a diagram (Fig. 87), showing the interactions of the major organisms in a saline habitat. Saline habitats and their assemblage of organisms could be considered ecological communities, since their organisms show a certain amount of interdependence and function somewhat as a unit. However, as can be seen from Figure 87, there is also an intimate connection between the saline habitat and the surrounding prairie. Because of this, the saline habitat should more properly be called a minor community.

TABLE 8. Arthropods, other than *Cicindela*, seen and collected in saline habitats in the central United States.

- Crustacea
  - Isopoda
- Diplopoda
- Arachnida
  - Acarina (infesting *Cicindela*)
  - Araneida
- Insecta
  - Odonata
    - Libellulidae, Gomphidae, Aeshnidae, Coenagionidae
  - Orthoptera
    - Acrididae, *Trimerotropis* sp.
    - Tetrigidae, *Paratettix* sp.
    - Tridactylidae, *Tridactylus minutus*
  - Hemiptera
    - Gelastocoridae, *Gelastocoris oculatus*
    - Saldidae, *Pentacora signoreti*
    - Cydnidae, *Schirus cinctus*
    - Pentatomidae, *Rhytidolomia* sp.
  - Homoptera
    - Fulgoridae, *Scolops* sp.
  - Coleoptera
    - Cicindelidae, *Megacephala virginica*
    - Carabidae, *Agonoderus lineola, A. obliqulus, Anisodactylus* sp., *Aspidoglossa subangulata, Bembidion coxendix, Calosoma* sp., *Clivina dentipes, Cratacanthus dubius, Diplocheila assimilis, Dyschirius criddlei, Elaphrus ruscarius, Geopinus incrassatus, Harpalus amputatus, H. pennsylvanicus, Pogonistes planatus, Pterostichus sayi, Scarites substriatus, Selenophorus* sp., *Tachys* sp.
    - Omophronidae, *Omophron nitidus*
    - Staphylinidae, *Bledius* sp.
    - Histeridae, *Hister biplagiatus*
    - Meloidae, *Epicauta conferta, E. segmentata*
    - Tenebrionidae, *Eleodes hispilabris, E. opaca, Lobometapon* sp.
    - Scarabaeidae, *Cotalpa subcribrata*
    - Chrysomelidae, *Calligrapha sp., Leptinotarsa decimlineata, Monoxia puncticollis*
    - Curculionidae, *Cleonis angularis, Hypera punctata, Lixus* sp., *Ophryastes vittatus, Pantomorus pallidus, Phytonomus nigrirostris, Sphenophorus aequalis, S. australis, S. callosus, S. destructor, S. germari, S. parvulus, S. scoparius, S. venatus*
  - Diptera
    - Chironomidae
    - Ceratopogonidae
    - Culicidae
    - Tabanidae, *Chrysops vittatus*
    - Stratiomyidae, *Eulalia communis*
    - Bombyliidae, *Anthrax analis, Exoprosopa dodrans, E. sordida*
    - Asilidae, *Diogmites symmachus, Laphystia* sp., *Nerax* sp., *Proctacanthus milberti*
    - Dolichopodidae
    - Syrphidae, *Eristalis aeneus, Eupeodes* sp.

Otitidae, *Cheroxys latiuscula*
Ephydridae, *Ephydra* sp.
Sarcophagidae
Muscidae
Anthomyiidae

Hymenoptera
  Tiphiidae, *Pterombrus rufiventris, Myzinum quinquecinctum*
  Mutillidae, *Dasymutilla leda, D. occidentalis, D. quadriguttata, D. vesta, D. waco*
  Formicidae, *Crematogaster* sp., *Pogonomyrmex occidentalis, Prenolepis imparis*
  Sphecidae, *Ammophila varipes, Cerceris* sp., *Prionyx atratus, Stigoides unicinctus*
  Pompilidae, *Anoplius* sp., *Poecilopompilus interruptus*
  Andrenidae, *Calliopsis* sp.
  Anthophoridae, Eucerinae



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*toads, lizards, sparrow hawk, raccoon, badger

Fig. 87. Interrelations of the major organisms in a salt flat community (subdivided into bare flats and margin) and the surrounding prairie. The organisms that the arrows point to use those at the other ends for food.

Another sort of relationship between cicindelids and other animals is found in the closely related phenomena of mimicry and cryptic coloration, in which a species evolves to look or act like something inedible (or at least not high on the list of "preferred" foods) to a predator species. R. Shelford (1902) and Robinson (1903) discussed some instances of mimicry of tropical Asian cicindelids (*Tricondyla, Collyris, Cicindela*) by locustids, cerambycids, a sciomyzid fly, and wasps. Blickle (1958) reported that a species of tabanid in Florida resembles *C. dorsalis* in color and flight habits.

Townsend (1886) noted that the species that live in wooded areas, such as *C. sexguttata*, are often green and difficult to see, even when sitting on a log; while others that frequent bare soil (*C. macra*, *C. cuprascens*, *C. repanda*, *C. tranquebarica*, and others) are often the same color as their background. He also noted that the white elytral markings, rather than being conspicuous, break up the outline of the insect and make it even harder to see; and that the ventral coloration, not visible from above, is often more brilliant than the dorsum. Wallis (1961) also mentioned matching of the background color, citing the nearly white species, *C. lepida*, which inhabits light sand and whose shadow is often more conspicuous than itself. Fox (1910) noted the close resemblance of some species on the New Jersey coast to their background, but also noted that in two species, individuals sometimes occurred on the "wrong" background. N. L. Rumpp *(in litt.)* said that two subspecies of *C. willistoni (pseudosenilis* and *praedicta)* are not at all well camouflaged, being dark blue-green forms and occurring on white salt pans in the Mojave Desert.

I too have noted that individuals of many species are very difficult to detect against their natural background, particularly when they do not move. Of the approximately 80 species of *Cicindela* in the United States, over 50 have a rather dull (brownish, blackish, dark green) dorsal color, over 20 are dull in some parts of their ranges and bright in others, and only about five are consistently bright (of these, two are green woodland forms). Of about 35 species that I have collected, about 25 are well camouflaged, five are well camouflaged in some parts of their ranges or in certain polymorphic forms, and only a few do not match their background well. It is interesting that in some species which appear dull to the naked eye (e.g., *C. macra*, which appears brownish), the elytral color, when viewed through a microscope, is actually made up of spots of bright blue or green on a red background; if the blue or green spots are large, the beetle appears dark brown, and if they are small, the color is bright reddish brown.

It seems likely that many of the predators of *Cicindela* exert a selection pressure that results in the beetles resembling their background by the killing of ill-matched individuals. Many birds and insects are known to have color vision. Evidence that this occurs is found in the sparrow hawk pellets that I examined (see section on predators and parasites). Remains of *C. circumpicta*, which occurs in reddish, green, and blue color forms in Kansas, were present; all were of green individuals, even though over 60% of the individuals are reddish in that area.

The pattern of geographic variation of color in some species (particularly *C. togata*) has led me to hypothesize that certain species of saline habitats respond to two selection pressures: one, to match the color of the soil in their local area; and two, to match the white of the salt. As noted in the section on saline habitats, in dry weather saline habitats become covered by a crust of crystalline salt; however, in wet weather the salt dissolves and the color of the underlying soil appears. Thus, the *Cicindela* of these habitats live on a substrate that frequently changes color. In many of the species in this study (*C. circumpicta*, *C. cuprascens*, *C. hirticollis*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*), I have noticed a definite correspondence between the dorsal coloration and the color of the soil in the locality. This is investigated more thoroughly in later sections. In the most nonfluvial species, *C. togata*, there is a decrease in the amount of white on the elytra in the eastern parts of the range, where the climate is more humid; while the southwestern part of the range, where the soil is more often dry, the white of the elytra increases. In one locality in western Texas, where the soil is nearly white, the elytra are almost completely white. This great tendency of some species to match their background can sometimes be used as a clue to past dispersals or ranges of these species.

In most species, the dorsum of the abdomen (as well as the venter of the body) is a bright metallic color, usually green or blue, even if the rest of the dorsum is dull. When the beetles fly, this bright area of the body is suddenly visible as the elytra are raised. It is possible that this acts as a flash or startle coloration to predators.

The species in this study exhibit certain morphological, physiological, and behavioral traits, or adaptations, for living in saline habitats, listed in Table 9. Some species have more or different adaptations than others. Since few

Table 9. Important morphological and behavioral traits for living in saline habitats (L=found in larvae also). Not all traits are necessarily found in all species studied.

Those shared with species not found in saline habitats;

1. Inactivity during the least favorable parts of the year (winter, summer); L.
2. Dig burrows to withstand temporary harsh conditions (storms, daily temperature fluctuations).
3. Hide under vegetation, in cracks, etc., to escape heat.
4. Protective coloration (resemble color of substrate, white markings act as disruptive coloration).
5. Cuticle of adult and setae of larvae protect from salt.
6. Reduction of competition (spatial and temporal segregation), L.
7. Able to be active at high temperatures; L.

Those found primarily in species of saline habitats:

8. Long legs:
    a. For rapid running to catch prey and escape enemies.
    b. To elevate body higher above hot substrate.
9. Increased white markings and body setae; L.
10. Tend not to fly because of high winds.

of the adaptations are restricted to species of saline habitats (even increased white on the body is found in some species living on light sand), probably few evolutionary changes were necessary for these species to become adapted to saline habitats. Those modifications that are necessary apparently have developed repeatedly, for many relatively unrelated species or species groups throughout the world are found in saline habitats. The first-listed adaptation, inactivity during the least favorable parts of the year, could be either an advantage or a disadvantage; if a species could become adapted to being active during the hot, dry summer, it could avoid competition from other cicindelids, provided there was sufficient food to make this a "worthwhile" expenditure of energy.

The literature is replete with notes about habitats in which adult cicindelids are found, and no attempt will be made to review them all. Blanchard (1921) found definite habitat preferences for 11 species in Michigan, and Fox (1910) did the same for 11 species in New Jersey. Sherman (1908) noted different species occurring at different elevations in western North Carolina. Vaurie (1950) gave brief habitat notes for 27 species in north central North America. In general, some species are found in quite restricted habitats, while others frequent many types of habitats. Such factors as the type and moisture of the soil, amount of vegetation, disturbance of the habitat, and climate are important in determining whether a species will inhabit an area.

One notable characteristic of many saline habitats in the central United States is that they support numerous species and individuals of *Cicindela*. On one June morning I collected 11 species (some being abundant) within an area of about one acre on a large salt flat in Woods County, Oklahoma. This is one extreme, but many habitats have five or more species. According to the competitive displacement principle (Gause's law), different species having identical ecological niches cannot coexist for long in the same habitat (DeBach, 1966); therefore, one naturally wonders how all these species can exist together, since all are general predators of about the same size, and since food appears to be scarce in saline habitats. By collecting throughout the warm months and noting the distribution of species in a particular saline habitat, I have found that there is a tendency for the species to be separated both spatially and temporally.

Spatial segregation is effected by the preference of various species for different microhabitats. This phenomenon is shown graphically in Figure 88, where species most likely to be active at the same time of year are grouped together. Clearly, some species, (*C. cuprascens*, *C. duodecimguttata*, *C. hirticollis*, *C. macra*, *C. nevadica*, and *C. repanda*) "prefer" moist conditions, one (*C. togata*) is most common on bare salt flats, one (*C. fulgida*) is common in dry, vegetated areas, and others (*C. circumpicta*, *C. punctulata*, and *C. willistoni*) are found in a variety of habitats. Another sort of spatial segregation

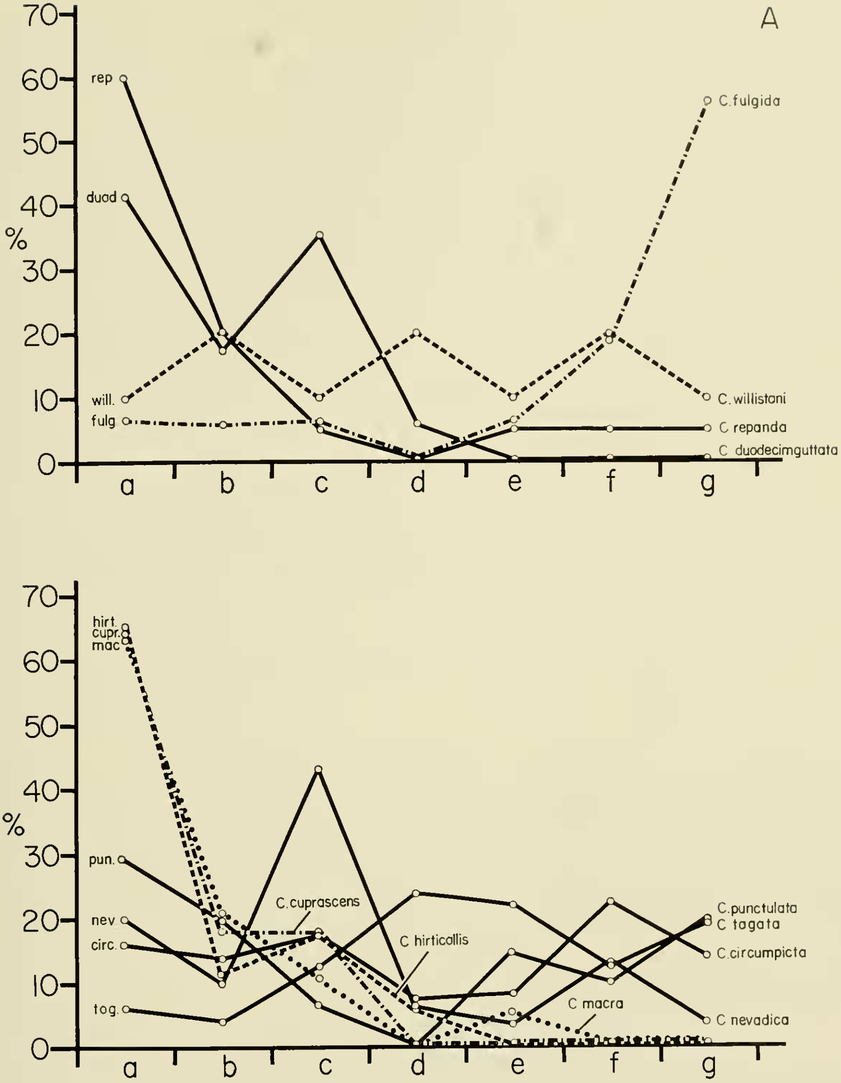

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Fig. 88. Per cent of instances in which the species were noted in various microhabitats, arranged from wet to dry and vegetated; A=spring and fall species; B=summer species; sample sizes range from 10 to 80, most being above 15; microhabitats: a=near water, or sand bar, b=low wet area, or moist ditch, c=near creek, or creek bank, d=moist bare salt flat, e=dry bare salt flat, f=small flats, or near margin, g=near hummocks, or among vegetation.

is found in differential soil preference. One species *(C. duodecimguttata)* is nearly always found on clayey soil, while some *(C. cuprascens, C. hirticollis,* and *C. macra)* occur on sandy soil. The others seem to have no "preference" and are found on both types of soil.

Temporal segregation is shown in Figure 89, where nonfluvial and fluvial species are grouped together. Some species *(C. duodecimguttata, C. fulgida, C. repanda,* and *C. willistoni)* emerge in the spring after hibernating as adults, mate, oviposit, and die out during the summer; in the fall a new brood of adults emerges. In other species *(C. circumpicta, C. cuprascens, C. hirticollis, C. macra, C. nevadica, C. punctulata,* and *C. togata),* the adults emerge during the summer, often nearly all at once *(C. nevadica),* and sometimes show a lull during the hottest months and a smaller emergence in the fall *(C. circumpicta).*

No diurnal temporal segregation was observed. Adults seem to be active throughout the day in fair weather when the air temperature is above 20° C and below 37° C. One would expect to find from a careful study that the spring and fall species are active at lower temperatures than summer species (see below). This could produce some diurnal temporal segregation during parts of the year when these two types of species occur together.

Although the temporal and spatial segregation are only partial, the combination of the two provides nearly complete separation of some species and

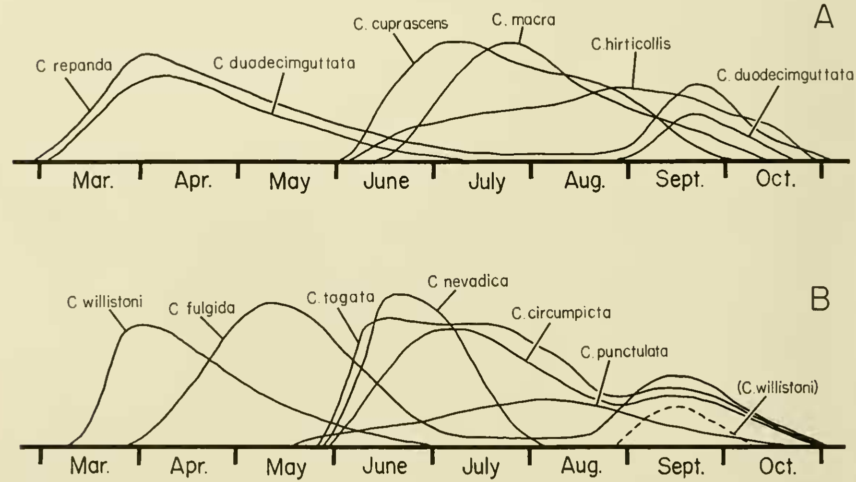

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FIG. 89. Relative abundance of the species throughout the year, generalized from data from localities in southern Kansas and northern Oklahoma; A=fluvial species, B=nonfluvial species; the exact positions of the peaks and ends of the curves, and their heights vary from year to year and at different localities and latitudes; *C. willistoni* has not been collected in the fall, but should be active.

partial separation of others, thus considerably reducing the possibility of competition. No organized data were collected on the subject, but casual observations indicated that food is the most important resource of the environment that is in short supply. Small arthropods suitable for food are usually very uncommon in saline habitats, and only very rarely was an adult or larva seen eating. Since the larva is the primary feeding stage and lives much longer than the adult, no doubt competition for food is even more severe among larvae than adults; furthermore, adults often occur in the same microhabitats as larvae and thus compete with them. Perhaps the long life of larvae and their habitat of lying in wait for prey at night are evolutionary "efforts" to reduce larval-adult competition. Insufficient data are available for the larvae, but it appears that those of most species are active at the same times of year as the adults; however, in species whose adults emerge only in the summer, the larvae are active in the spring as well. Many larvae of *C. togata* are active throughout the hottest part of the summer, when the larvae of most species are inactive (i.e., have their burrows plugged).

Another resource that could be in short supply for species frequenting marginal microhabitats is space, initially for oviposition sites, but ultimately space for larval burrows. Many times I have seen favorable larval sites literally riddled with larval burrows.

If competition among species of *Cicindela* is important, one would expect to find fewer species in habitats with fewer or less abundant resources. In Table 10, the number and abundance of species in 14 saline habitats with varying types and abundance of microhabitats are compared. Those habitats with many microhabitats, abundant water, and a large area have more species which are more abundant than the more impoverished habitats. There are other possible reasons why certain of the habitats in Table 10 have fewer species than others: some are fluvial habitats and would have few if any nonfluvial species; and some of the habitats are outside the ranges of some species. However, it is likely that the "preference" of different species for different microhabitats and the differing ranges of species evolved at least partly because of competition.

Some of the effects on *Cicindela* of physicochemical factors of the environment have been alluded to above. The primary factors that govern the activity of adults seem to be temperature, humidity (actually evaporation), probably light, and wind. Shelford (1913b) found that *C. scutellaris* reacted negatively to dry air and positively to moister air, and that beetles moved against a stream of warm air (in the laboratory). Chapman et al. (1926), in a study of sand dune insects in Minnesota, found that *C. formosa* and *C. lepida* become active at 15-20° C, and that *C. lepida* dies at 45-50° C and *C. formosa* at 50-55° C. They emphasized temperature and noted that the "successful" sand dune insects are able either to endure great extremes or

TABLE 10. Presence and abundance of various microhabitats at 14 saline habitats in southern Kansas and northern Oklahoma (O=absent, pluses indicate relative abundance), and number of species of *Cicindela* and their relative abundance at these habitats (N=total number of species).

Localities (nearest town)	Microhabitats				Number of species				
	Permanent water	Large, open flats	Dry margin or small flats	Short vegetation	Abundant	Common	Uncommon	Rare	N
Plainview, Okla.	+ + + + +	+ + + + +	+ + + +	+ + + +	3	1	1	4	11
Hudson, Kans.	+ + + +	+ + + + +	+ + + +	+ + + + +	4	1		2	9
Cherokee, Okla.	+ + + +	+ + + + +	+ + + +	+ + +	4	1	1	2	8
Hazelton, Kans.	+	+ +	+ +	+ +		2	3	1	6
Geuda Spgs., Kans.	+ + +	O	+	+			3	4	7
Drummond, Okla.	+	O	+	+		3		2	5
Belvidere, Kans.	+	O	+	+		2	2	2	6
Mayfield, Okla.	+ + +	O	+	+		2	1	3	6
Okeene, Okla.	+ + +	O	+	+			4	3	7
Guthrie, Okla.	+ + +	O	O	+	2	1		1	4
Orienta, Okla.	+ + +	O	O	O			2	1	3
Galva, Kans.	+	+	+	O		1		3	4
El Dorado, Kans.	+	+	+	O		2	1	1	4
Greenwich, Kans.	O	+	+	O			1	1	2

avoid them by being active at other times. Rensch (1957) found similar ranges of activity for *C. hybrida* in Europe (25-45° C), *C. bicolor* in India (25-43° C), and *C. nilotica* in Egypt (27-37.5° C). He noted a few individuals of the latter species active on moist sand at 46° C, but never any on dry sand at 43-46.5° C. Remmert (1960) studied daily changes of light and temperature preference in *C. campestris* in the laboratory, finding that during the day the preferred temperature is 34.6° C, while at night it is 26.0° C; however, the temperature preference depends on the physiological state of the beetle: hungry and thirsty individuals have a lower preference than fed ones. His experiments indicated that the beetles are more positively phototactic during the day, but he did not keep temperature and humidity constant, and the results are not conclusive. Payne (1964) studied temperature preferences (humidity not controlled) of *C. repanda* and *C. rufiventris* in the laboratory. *C. repanda*, a spring and fall species, preferred 25-32° C, and *C. rufiventris*, a summer species, preferred 25-38° C.

I have made a few incidental measurements of temperatures at which *Cicindela* become active or cease activity in the field: *C. repanda* was seen "sunning" but not running about when the air temperature was 15° C; *C. duodecimguttata* became active at about 25° C; *C. willistoni* became active at about 18-19° C; *C. circumpicta* was active at about 21° C, and became inactive (in shade of vegetation) at about 36° C; *C. togata* was sluggish and unable to fly at 22° C; *C. punctulata*, *C. circumpicta*, *C. togata*, and *C. repanda* were found near water, in grass, in burrows, or in cracks in the soil at about 38-39° C. As mentioned above, I found *C. circumpicta* mating at night, probably because the habitat was too hot during the day; thus temperature seems to be more important than light in influencing activity. Adults of some species (*C. circumpicta*, *C. cuprascens*, *C. macra*, *C. nevadica*, *C. punctulata*, *C. schauppi* and *C. togata* in this study) also are attracted to artificial lights, making this a profitable means of collecting.

Another effect of temperature (as well as humidity) on adults of certain species was investigated by Shelford (1917). He found that the color and elytral pattern of the adult are affected by the temperature and humidity at which the prepupal and pupal stages develop. Individuals reared at high temperatures had more reduced markings (cover a smaller portion of the elytra) than those reared at low temperatures. Similarly, colors were brighter in dry conditions and darker in moist conditions. He noted that in some species, forms with bright colors and reduced markings occur in hot, dry areas, while forms with bright colors and expanded markings occur in areas of hot, moist climate. However, he noted the importance of microhabitat conditions, which still have not been studied or mapped well.

As mentioned above, strong wind reduces the tendency of some species to fly; when they do, they are often carried to unsuitable habitats. The other effects of wind have not been studied, but no doubt one is increase in rate of water loss, probably causing many species to seek protected microhabitats.

Cicindelids do not seem to be adversely affected by the high concentration of salts in saline habitats. Adults, as well as larvae, of at least some species are found in all parts of saline habitats that are not well vegetated or flooded. Apparently the thick exoskeleton of adults and the long spines and setae of larvae and pupae serve as a mechanical protection from salts.

The Adult—*Dispersal.* Besides being the reproductive stage, adult *Cicindela* are the dispersal stage of the species. The fluvial species, none of which is restricted to saline habitats, almost certainly disperse along streams. However, nonfluvial saline habitats are today separated by many miles of land that is unsuitable for species of saline habitats. Yet these species are found at most of them, including man-made ones near oil wells that could not have been in existence for more than 80 or 90 years. How has this dispersal taken place? Although most species of *Cicindela* are agile fliers, they rarely fly in nature unless disturbed by an animal larger than themselves. I have noted that in strong wind, when the beetles do fly, they sometimes lose control and go sailing out of sight over the prairie. Quite probably, strong winds are a factor in dispersal. Storms may or may not be important; adults usually take cover and become inactive in bad weather, although Woodruff and Graves (1963) thought hurricanes might have been responsible for the introduction of a Cuban species into Florida. Between the major saline habitats are scattered many small salty patches, not ideal habitats for large populations of *Cicindela*, but able to support small numbers. Such areas no doubt form "stepping stones" for dispersal between major saline habitats. For example, I have found small populations of *C. circumpicta*, *C. fulgida*, *C. nevadica*, and *C. togata* in small salty spots in pastures and fields. Another factor in some cases is that some nonfluvial saline habitats are interconnected by streams. Species that "prefer" salt flats have occasionally been found on sand bars of streams and evidently disperse along them.

After some beetles have dispersed to a saline habitat, what are the factors that determine whether they can survive there, and if so, how numerous can they become? One of the most important factors is that the soil be of the proper type and moisture content for larval development. Many small salty patches in pastures and roadside ditches become too dry in the summer for the larvae of most species. In some parts of the country (the desert Southwest), extremes in temperature might be a limiting factor, but in the central United States, most species escape unfavorable temperatures by becoming inactive or seeking a microhabitat that is more equable. However, there are some species in the northern United States and western mountains (e.g., *C. pusilla*) which probably do not occur as far south or east as Kansas at least partly because of high temperatures. The availability and abundance of food are obvious and important limiting factors, as is the amount of vegetation. Competition, discussed above, is another. No doubt a combination of these factors is responsible for the decrease in abundance and number of species on impoverished habitats noted above (Table 9). Salinity seems not to affect the beetles at all adversely, since they are found (larvae and adults) in all bare parts of saline habitats.

Man has no doubt had a great effect on the distribution and abundance of cicindelids. By altering or destroying habitats, such as cutting forests or plowing prairies, he has restricted the distribution of some species and made it possible for others to expand. Dirt roads, paths, road cuts, eroded gullies, vacant lots, field edges, etc., provide favorable habitats for colonization by some species, such as *C. punctulata*. Similarly, the construction of farm ponds, lakes, and irrigation canals has probably aided species that live near water. On the other hand, increased use of insecticides, housing developments, polluted waterways, and the damming of rivers has undoubtedly adversely affected some species.

Man has also affected many saline habitats. Agricultural activities may lead to silting in of saline habitats in natural depressions. Schaffner (1898) said that a salt marsh in Republic County, Kansas, had suffered much in this manner already by 1897, being much smaller than it formerly was and having only several hundred acres without vegetation. Today, nearly the entire area is vegetated, some is being used for raising crops, and during the course of this study, a marshy area (Fig. 7) was drained and an unsuccessful attempt made to grow crops on it. As mentioned above, man may also create saline habitats by irrigation or drilling for oil. Fender (1945) reported finding one specimen of *C. cuprascens* (dead) and several of *C. punctulata* (three alive) in McMinnville, Oregon, in mail sacks from Council Bluffs, Iowa. These species are attracted to lights and must have fallen into the mail sacks at night. Thus, any species coming to lights may be transported considerable distances by man under favorable circumstances. Also, the larvae of any species could conceivably be transported by man in loads of soil.

THE LIFE CYCLE. Only a few of the world's species of cicindelids have had their life cycles worked out completely or even in part. Development takes one to several years, and some species do poorly under laboratory conditions, making them difficult to rear. Enock (1903) and Huie (1915) worked out the four-year cycle of *C. campestris*. Criddle (1910) studied the cycles of *C. limbata*, *C. limbalis*, *C. formosa*, and *C. lengi* in the field. Shelford (1908) worked out the cycles of *C. punctulata*, *C. purpurea*, *C. lepida*, *C. limbalis*, *C. formosa*, and *C. sexguttata* from laboratory and field observations and gave partial cycles for other species. Zikan (1929) reared many Brazilian species in several genera partly through their cycles. Shelford (1908, 1911) noted that temperature, moisture, climate, and food influence the length of

TABLE 11. Life cycles of *Cicindela* worked out by previous authors (Criddle, 1910; Shelford, 1908; Huie, 1915). Only one possible cycle is shown for each species; larval stages may be lengthened. The exact times of appearance of the stages varies geographically and from year to year. A=adult; O=oviposition; 1L, 2L, 3L=first, second, and third larval instars; P=pupa; ....=hibernation.

	1 year cycle (*C. punctulata*)	2 year cycle (*C. purpurea*)		2 year cycle (*C. lepida*)		3 year cycle (*C. lengi*)			4 year cycle (*C. campestris*)			
April	3L	A	3L	3L	2L	A	3L	3L	A	2L	3L?	3L
		0				0			0			
May		1L		P		1L						
	P								1L			
June								P				
	A	2L		A	3L							
	0			0		2L						
								A				P
July			P							3L?		
	1L	3L		1L								
									2L			
August	2L		A									A
				2L								
						3L						
Sept.	3L											
Oct.												

the different stages of the life cycle, particularly the larval stages; thus some of the species that Shelford studied at Chicago were found by Criddle to have longer life cycles in Manitoba, Canada. This, plus the facts that life cycles are long and adults oviposit for a number of weeks or months, often gives rise to great overlaps and a heterogeneity of cycles for a species. In general, two major types of life cycles can be delimited. In the first, adults emerge from the pupa in the fall, feed, hibernate, become active in the spring, and oviposit; variable larval stadia may produce a two to four year cycle. In the second type, adults emerge in the early summer and oviposit soon thereafter, dying off before winter; the total life cycle may last one to two years. The life cycles worked out by the above authors are shown diagrammatically in Table 11.

I succeeded in rearing only one individual of *C. togata* completely through its life cycle. Adults of *C. togata* were collected from Lincoln County, Kansas, on 7 September 1963, and kept in a laboratory terrarium. Several days later they began ovipositing. First instar larvae were first seen on 24 September 1963; on 28 January 1964, the larva that was eventually reared became a second instar larva; and on 20 April 1964, it became a third instar larva. The third instar burrow was last closed on 20 July 1965. An adult female, with elytra still soft, dug its way out of the soil on 6 September 1965, two years after the adults were collected. This evidence, plus observations on larvae in

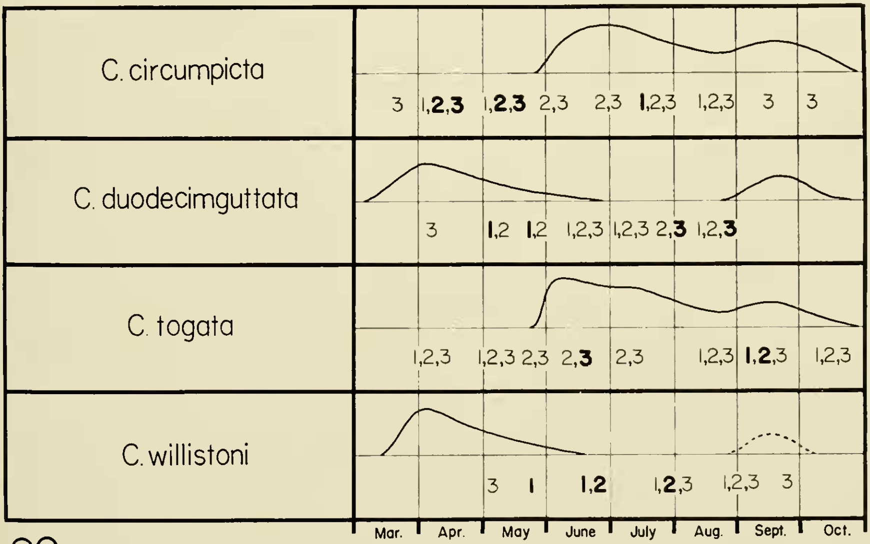

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FIG. 90. Temporal distribution of larvae of different instars (1=first, 2=second, 3=third) and adults (height of curve indicates relative abundance) of four species of saline habitats. A boldface number indicates that the instar was very abundant.

the field, leads to the conclusion that the life cycle takes two years (but may be lengthened to three), and is similar to that of *C. lepida* in Table 11. Larvae apparently hibernate in any of the three instars (Fig. 90).

In Figure 90 are shown times of the year that I have seen or collected larvae of different instars of four species. From these data and the times of adult activity, certain tentative conclusions can be drawn about the life cycles: *C. circumpicta* appears to have a life cycle similar to that of *C. togata*. *C. duodecimguttata* and *C. willistoni* probably have cycles similar to that of *C. purpurea* in Table 11; however, from the temporal distribution of larval instars, their cycles may only take one year.

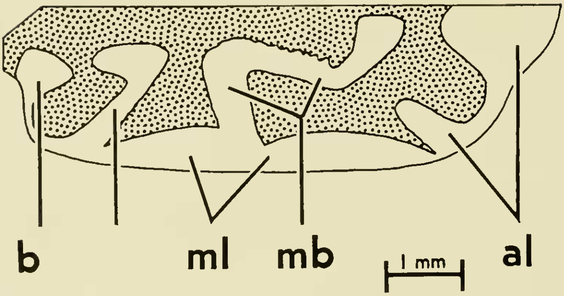
ZOOGEOGRAPHY OF *CICINDELA* OF SALINE HABITATS

Zoogeography is a very broad field of study, drawing its data from the disciplines of ecology, systematics, phylogeny, paleontology, paleoclimatology, physical geology, pedology, and geography. Zoogeography may be defined as the study of the distribution of animals in space and time, how and why this distribution came about, and prospects for future changes. Discussions of the principles and methods of zoogeography can be found in Darlington (1957) and Munroe (1963).

Many papers have appeared recently on the zoogeography of North American insects; e.g., Gressitt (1958), Howden (1963), Linsley (1939, 1958), Miskimen (1961), Rhen (1958), Ross (1953, 1958), and Ross and King (1952). The results of some of these can be applied to cicindelids. Works dealing with the zoogeography of cicindelids are fairly numerous. Horn (1908-1915) made speculations on the phylogeny and past dispersal of the family, but he was hampered by the relatively incomplete geological knowledge of the time. Rapp (1946) listed the distribution of the cicindelid genera on the seven major land masses of the world and hypothesized about their origin and dispersal. Crowson (1946) quickly criticized some of Rapp's conclusions. Kolbe (1935) expounded his theory of "morphological progressive animal dispersal," using the palearctic species *C. lunulata* as an example; the theory proposes that the most primitive forms occur at the place of origin and the most advanced at the periphery of the range. This is similar to the "age and area" hypothesis of J. C. Willis (see Darlington, 1957). Mandl (1954), studying the male genitalia of many of the cicindelid genera, hypothesized about their evolution and dispersal. Papp (1952), in a study of the male genitalia of 33 North American species of *Cicindela*, placed the species into groups of close relatives, noted the existence of close relatives in the palearctic region, and drew general conclusions about the evolution and dispersal of the North American cicindelid fauna. Schilder (1953b) subdivided the classical *Cicindela* into 18 genera and 29 subgenera, based at least partly on distribution, and speculated about their evolution and dispersal. Rivalier (1950, 1954, 1957, 1961, 1963) published a much more "natural" classification of the classical *Cicindela* (also subdividing it into genera) based primarily on the male genitalia. Ihering (1926) speculated about the dispersal of *Megacephala carolina*. Van Dyke (1929, 1939), in more general papers on North American Coleoptera, mentioned the faunal affinities of *Megacephala*, *Amblychila*, and *Omus*. Leconte (1875a, 1875b) proposed that the occurrence of *C. hirticollis* and *C. lepida* in similar habitats along the Atlantic coast and in the interior of North America could be explained by assuming that the inland populations are remnants of populations that lived on the shores of Cretaceous seas. Wickham (1904a, b) speculated on the evolution of *C. willistoni* and correlated its supposed evolution and dispersal with geological events. Shelford (1907) noted the preference of *C. sexguttata* for oak-hickory forests and predicted that as most forests of northeastern North America changed to a beech-maple climax (man eliminated), this species would be driven out of the area. Leng (1912) discussed factors controlling the distribution of the species of *Cicindela* of eastern North America: temperature, mountain barriers, local environment, behavior and adaptability of the species, accidents of climate and geological changes, and place of origin. Cazier (1948) treated the origin and dispersal of the cicindelid fauna of Baja California, Mexico, as it was known then. In a later publication (1954), he grouped the Mexican species of *Cicindela* according to their faunal relationships. Rumpp (1956, 1957, 1961) studied a number of species in the southwestern United States, including *C. willistoni*, *C. nevadica*, *C. fulgida*, *C. circumpicta*, and *C. togata*, and correlated their possible evolution and dispersal with geological events. Freitag (1965) postulated phylogenetic and zoogeographic schemes to explain the distribution, geographic variation, and systematics of nine North American species, particularly *C. duodecimguttata*, *C. oregona*, and *C. depressula*.

In this work, seven species were studied in detail zoogeographically: *C. circumpicta*, *C. cuprascens*, *C. fulgida*, *C. macra*, *C. nevadica*, *C. togata*, and *C. willistoni*. Brief mention will be made of other species. Each species will be discussed individually.

Methods. Data from several sources were used. The present known distribution of the species was determined by personal collecting and from records from the literature and museum collections. Geographic variation was studied statistically. Samples of specimens from various localities, assumed to have been collected at random, were measured. External morphological characters were used, such as lengths and widths of body parts, shapes of the white elytral maculation, and color. Males and females were studied separately. Size measurements were taken using an eyepiece micrometer in a binocular dissecting microscope and were later converted to millimeters.



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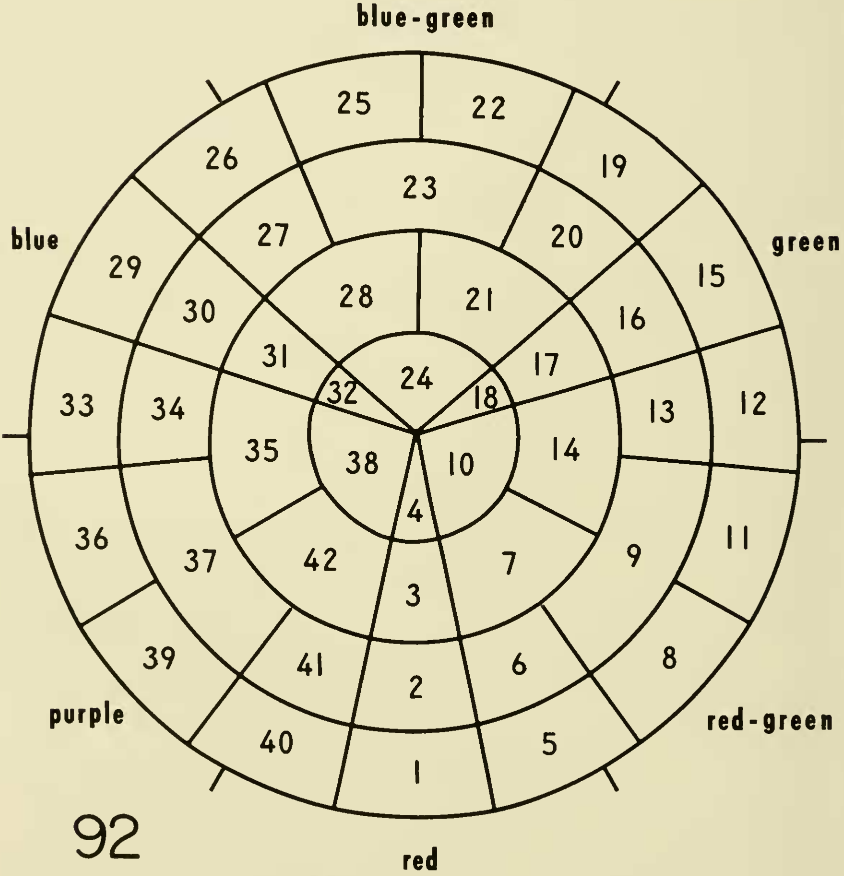

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FIG. 91. Left elytron of *C. cuprascens* (dorsal aspect), illustrating terminology of the maculation: al=apical lunule; b=basal dat, hl=humeral lunule, mb=middle band, ml= marginal line. FIG. 92. Color wheel used to study geographic variation of elytral color in five species of *Cicindela*. The brightest (most saturated) colors are around the rim; dark colors are toward the center, with black being at the center. The numbers are used for later reference. The marks outside the rim divide the wheel into six sectors for more simplified representations.

The possible shapes of the elytral maculation were subdivided into several arbitrary states, which were given numbers; specimens were then scored in decimal fractions of these states. The terminology used with the maculation is as follows (Fig. 91). The maculation is quite variable; however, a typical pattern consists of a humeral lunule (with or without a basal dot), middle band, and apical lunule. These markings may be connected at the margin by a marginal line. From this pattern the markings may be reduced to dots or complete absence, or they may be fused until the elytra are white or nearly so.

In the case of *C. togata*, variations of elytral color could be arranged in a linear series and represented by a scale of numbers; color was then treated as any other character. However, in the other species (except *C. fulgida*, for which color was not measured because of the temporal change of color noted in the section on adult post-emergence changes), the range of colors is more complex and had to be studied separately from the other characters. The possible colors, with but few exceptions, could be arranged in a color wheel (Fig. 92), with bright green, blue, and reddish at equidistant points at the edge, intermediate colors between them (blue-green, purple, red-green), and darker shades of the same colors toward the center (black being at the center). The color wheel was subdivided into 42 sections (numbers in Figure 92), and specimens were found which fit into all of them. The names of these colors, in the Ridgway (1912) and Inter-Society Color Council-National Bureau of Standards (Kelly and Judd, 1955) systems are given in Table 12. Specimens were examined against a white background with the naked eye, using overhead lighting from Sylvania cool white fluorescent bulbs. With the eye perpendicularly above the elytra, the position the specimen occupied on the color wheel was determined and a dot made on a data sheet with an outline of the wheel and its sections. Viewing such a sheet, with many dots representing a sample from a given locality, gives one an idea of the "color structure" of that population. For the purpose of comparing many populations on a map, a simplified, less detailed version of the color wheel was used because of space limitations on the maps.

The measurements, except those involving the color wheel, were analyzed, using an IBM 7040 computer, by the method of multivariate generalized discriminant functions. The computer program, available at the Computation Center of The University of Kansas, was written by Dr. F. James Rohlf, University of Kansas. It is called MULDIS, short for multigroup discriminant functions. The theory of generalized functions is explained in Jolicoeur (1959) and Seal (1964), where it is referred to as "canonical analysis." In brief, the method consists of a simultaneous analysis of the characters of specimens drawn from a number of localities. Any differences that exist among the groups of specimens can be displayed in the most efficient man-

TABLE 12. Color names of the sections of the color wheel (first column) in the Ridgway (1912) and Inter-Society Color Council—National Bureau of Standards systems. The names and numbers of the latter system often have greater latitude than those of the Ridgway system, accounting for duplication.

Section	Ridgway	ISCC-NBS
1	Brick red	strong reddish brown (40)
2	Hay's brown	moderate reddish brown (43)
3	Clove brown	dark grayish reddish brown (47)
4	Chaetura drab	brownish black (65)
5	Russet	strong brown (55)
6	Prout's brown	strong brown (55)
7	Natal brown	grayish brown (61)
8	Cinnamon brown	moderate brown (58)
9	Saccardo's olive	dark olive brown (96)
10	Dark olive	dark olive brown (96)
11	Dresden brown	light olive brown (94)
12	Forest green	deep yellow green (118)
13	Roman green	moderate olive green (125)
14	Dark dull yellow green	moderate olive green (125)
15	Cossack green	deep yellowish green (132)
16	Varley's green	dark yellowish green (137)
17	Danube green	dark green (146)
18	Dusky olive green	very dark yellowish green (138)
19	Meadow green	strong green (141)
20	Bottle green	deep green (142)
21	Duck green	very dark green (147)
22	Dark viridian green	strong green (141)
23	Invisible green	dark bluish green (165)
24	Dusky dull green	very dark bluish green (166)
25	Wall green	deep bluish green (161)
26	Myrtle green	deep bluish green (161)
27	Dusky green-blue (1)	dark greenish blue (174)
28	Dusky dull bluish green	very dark greenish blue (175)
29	Alizarine blue	deep blue (179)
30	Dusky orient blue	deep blue (179)
31	Dark delft blue	dark blue (183)
32	Bluish slate-black	dark blue (183)
33	Dark aniline blue	deep purplish blue (197)
34	Dull violet-black (3)	dark purplish blue (201)
35	Dull purplish black	dark violet (212)
36	Burnt lake	very deep purplish red (257)
37	Dusky auricula purple	very dark red (17)
38	Blackish violet-gray	blackish purple (230)
39	Vandyke red	dark red (16)
40	Madder brown	dark red (16)
41	Diamine brown	very deep red (14)
42	Dark mineral red	very deep red (14)

ner. One means for doing so is to transform the locality means into specially standardized units, so that the means of the localities can be plotted as points in an n-dimensional hyperspace, where n=number of characters, or number of localities -1, whichever is the smaller. The coordinate axes (generalized discriminant function) of these points are constructed so that the greatest amount of variance among localities (relative to that within localities) is explained by the first discriminant function, the next greatest amount by the second function, etc. Chi square tests are performed on each function; nonsignificant functions are ignored. A matrix of generalized distances is produced, giving the distance from the mean of one locality to that of any other; the greater the distance, the more different the specimens from the compared localities in the characters measured. One can also perform analyses of variance (anova) on each character with intermediate output of the program. A test is also made for homogeneity of the variances of the groups.

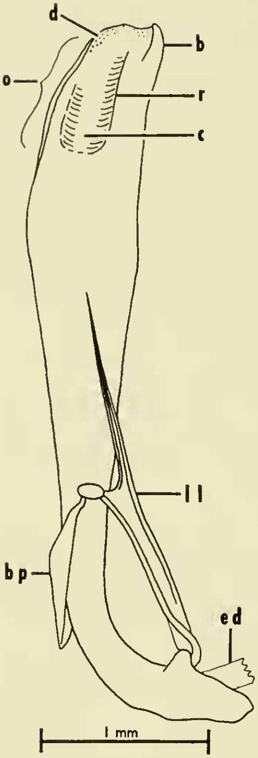
The significance of the differences in position of the means of the localities in n-dimensional hyperspace was tested using an unpublished method of Dr. K. R. Gabriel, called "likelihood ratio manova simultaneous testing procedure" (STP). Program 6, option D, available at the Computation Center of The University of Kansas, was used. In this method, the probability of making a type I error (that is, rejecting a true hypothesis) is known; a value of 5% was used. This is an experiment-wise error rate; a type I error will be made in 5% of the studies, or experiments. Another characteristic of this method is that if a certain set of means is found to be not significantly different, no subset within it will be significantly different.

Inferences about the phylogeny of the species studied were drawn from the literature, particularly Rivalier (1954), and from the results of this study. The grouping of species by Rivalier (1954) was used as a basis for the systematic arrangement of the North American fauna of *Cicindela*; however, it was found that certain minor corrections were necessary, on the basis of examination of the male genitalia of certain species. Mandl (1954) gives instructions for the preparation and observation of the male genitalia; however, in his method the inner sac is everted, making it difficult to see the interrelationships of the various internal parts. Freitag (1965) gave very brief instructions. The method I have developed is as follows:

1) If working with dried specimens, relax them for at least a day, or use a relaxing fluid.

2) Holding the beetle upside down, reach inside the genital opening with fine-pointed forceps and gently remove the aedeagus (it is best to use a low power dissecting microscope). Choosing specimens with the aedeagus partly extruded makes this easier. It may be necessary first to separate the aedeagus from the sclerites around the anus, to which it often adheres because of dried body fluids. Be careful that the curved proximal part does not break or that the basal piece and lateral lobes do not become separated.

3) Place the aedeagus in a 10% potassium hydroxide (KOH) solution for about 5-10 minutes to dissolve the tissue that usually adheres to the proximal part. Transfer it to a small Stender dish or microscope slide with a small amount of water and remove any remaining tissue with forceps. A weak acetic acid bath may be used to stop the action of the KOH.



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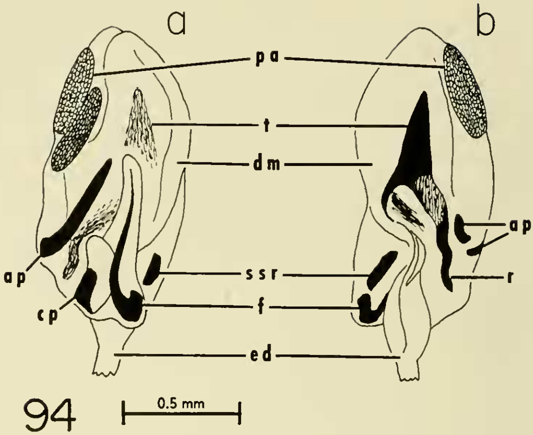

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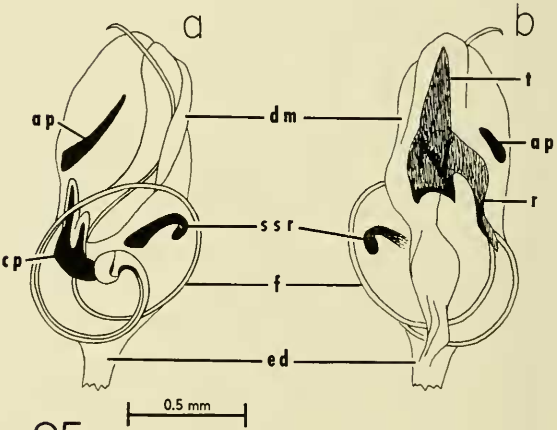

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FIG. 93. Aedeagus of *C. cuprascens* (Douglas County, Kansas), dorsal aspect. Abbreviations: b="beak," bp=basal piece, c=concavity, d=denticles, ed=ejaculatory duct, ll=lateral lobes (only one is drawn), o=orifice, r=ridge. FIG. 94. Inner sac of aedeagus of *C. fulgida* (Stafford County, Kansas); a, dorsal aspect; b, ventral aspect. Abbreviations: ap=arciform piece, cp= central plate (partly weakly sclerotized), dm=denticulate membrane, ed=ejaculatory duct, f=flagellum, pa=paired areas with large denticles, r=rod, ssr=small stiffening rod, t=tooth. FIG. 95. Inner sac of aedeagus of *C. cuprascens* (Douglas County, Kansas); a, dorsal aspect; b, ventral aspect. Abbreviations same as in Fig. 94.

4) Place the aedeagus on its "dorsal side" (as it lies at rest in the beetle) and make a drawing of it (see Fig. 93). This is best done with a camera lucida or ocular grid and graph paper. Note ridges, concavities, and denticles near the distal end. Also note the shape (curvature, thickness, etc.) of the entire aedeagus and of the heavily sclerotized part (often beak-shaped) at the apex, as well as the relative length of the lateral lobes. Sometimes a useful character is found by viewing the apex from the "side"; *i.e.,* from the direction of the orifice. Add a millimeter scale beside the drawing.

5) Slit the aedeagus longitudinally from about the middle to the apex. A scalpel or razor blade might work for this, but I used an insect pin with the point bent into a tiny hook, the pin

mounted in a wooden handle. Hold the proximal part of the aedeague with forceps and push the insect pin into it proximal to the inner sac to make a starting hole. Then pull the tool toward the apex, being careful not to poke it deep inside, using the hook to tear a slit. If the aedeagus is heavily sclerotized, this operation may be difficult.

6) Holding the proximal part of the aedeagus with forceps, reach inside the slit near the middle of the aedeagus with a fine teasing needle or another forceps, grasp the ejaculatory duct proximal to the inner sac, and gently pull the inner sac out of the slit. It will be connected to the aedeagus at the orifice by membranous cuticle; the membrane should be severed with a scalpel or teasing needle, being careful not to tear it where it continues over the inner sac.

7) Place the inner sac in a 10% KOH solution for 5-10 minutes, immerse it briefly in an acetic acid bath, remove it to a slide, and remove excess tissue with forceps, exposing the sclerotized membranes and pieces that compose the inner sac. The great complexity of these parts makes them difficult to draw. Make drawings from the dorsal and ventral aspects and any others that clarify the shapes and interrelationships of the parts. The sclerotized pieces are covered by membranes, often produced into complex folds; some parts of the membrane are transparent and some are covered by denticles of various sizes. The size and distribution of denticles is often an important character, usually more so among species groups than among closely related species. The sclerotized pieces show the most important characters; they vary widely in shape within the genus *Cicindela*, but they can usually be homologized from one species to another (see Rivalier, 1950-1963). Two examples, one of a more primitive species and one of a more advanced species, are shown in Figures 94 and 95. One can often see the parts of the inner sac more clearly if it is examined (by transmitted light) immersed in glycerin rather than water.

8) Keep all parts in glycerin in a corked microvial on the pin of the specimen.

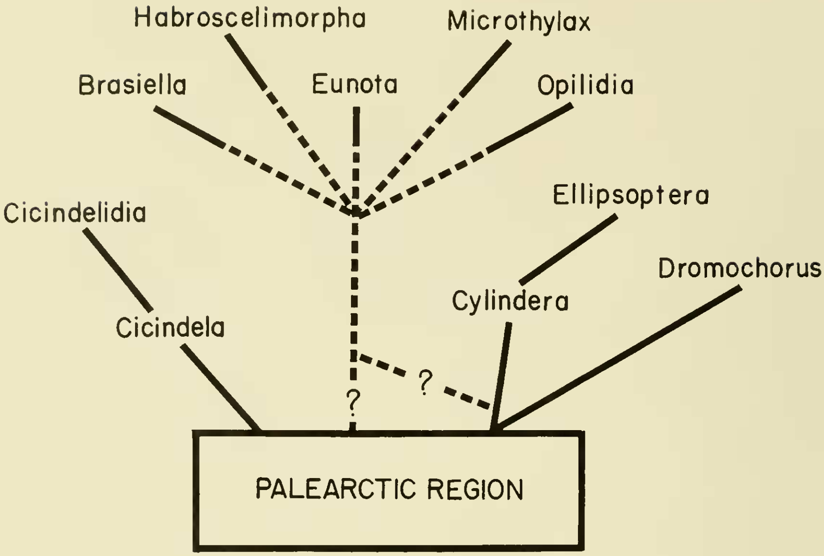
9) Examine the genitalia of at least several specimens of a form to determine the range of variation of the characters.

10) Be certain that the aedeagi and inner sacs are oriented the same way for drawings; a slight rotation can change the appearance of many parts.

PHYLOGENY

Unfortunately, few fossils of cicindelids are known. Horn (1906) discussed a *Megacephala* from the Baltic amber, which he said was conspecific with the modern American *M. carolina*, and hypothesized about how it happened to get there; however, Cockerell (1920) though that this specimen was a fake. Cockerell (1920) described a fossil, represented only by an elytron, from White River, Colorado (Green River age), as *Cicindelopsis eophilus*; however, as he pointed out, it does not have an inner apical elytral angle as do known cicindelids, and it may be from a cerambycid. G. Horn (1876) discussed two species of fossil *Cicindela* from a post-Pliocene cave at Port Kennedy, Pennsylvania. He said one is *C. haemorrhagica*, a species now restricted to the southwestern United States and northwestern Mexico; he did not name the other species. A close relative of *C. haemorrhagica*, *C. rufiventris* now occurs east of the Rockies; Horn could have misidentified the specimen.

Consequently, conclusions about the phylogeny of cicindelids must be drawn almost entirely from the present fauna. Earlier attempts to make phylogenies, e.g., Horn (1908-1915) and Schilder (1953b), were based on external morphological characters, particularly the elytral maculation in *Cicindela*. Mandl (1954) produced a much more satisfactory scheme (although fragmentary) for the family, using the male genitalia in addition to external characters. Papp (1952) arranged the species that she studied into



Cicindela

- C. hirticollis
- C. duodecimguttata
- C. repanda
- C. fulgida
- C. tranquebarica

Cicindelidia

- C. willistoni
- C. punctulata
- C. schauppi

Habroscelimorpha

- C. circumpicta

Eunota

- C. togata

Ellipsoptera

- C. nevadica
- C. cuprascens
- C. macra

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FIG. 96. Proposed scheme of evolution of the North American fauna of *Cicindela*. Names are the "genera" of Rivalier (1954). The species in this study are listed under their respective "genera" at the bottom.

groups progressing from phylogenetically old to young, as did Rivalier (1950-1963) in his more complete work. Rivalier made few statements about the actual phylogeny of his groups except for some remarks in his last paper (1963). From the meager comments of Mandl (1954), Papp (1952), and Rivalier (1963), and from the excellent systematic arrangement of Rivalier, it is possible to speculate on the phylogeny of the *Cicindela* of North America.

The family Cicindelidae and the genus *Cicindela* probably arose in Africa (Mandl, 1954). From there, secondary centers of evolution in the Old World tropics were colonized. Population of the New World by *Cicindela* probably occurred only from the north, via the Bering land bridge (although Mandl, 1954, thought that other genera dispersed to the New World at an earlier time via a southern land bridge).[4] Much radiation occurred in the New World, producing many indigenous groups ("genera" of Rivalier). A hypothetical scheme of evolution, using the names of Rivalier's "genera" is shown in Figure 96. At least two major ancestral stems crossed the Bering land bridge. One was *Cicindela* s. s., a group found throughout the Old World as well. This "genus" gave rise to *Cicindelidia*, which is restricted to the New World. The other major stem was *Cylindera*, a group also found throughout the Old World. It gave rise to *Ellipsoptera* and *Dromochorus*, which are restricted to the New World. The remaining five "genera" are an endemic, heterogeneous group whose origin is more uncertain. Probably at least some of them evolved from ancestors that crossed the Bering bridge; others may have split off the *Cylindera* stem.

Because of the paucity of cicindelid fossils, it is difficult to date the evolution of *Cicindela*. According to Carpenter (1953), the earliest known beetle fossils are from late Permian strata; cicindelids probably arose at about this time. The evolution of most of the cicindelid genera probably occurred during the Mesozoic. Horn (1908-1915) thought that the genus *Cicindela* became differentiated in the early Tertiary and that the ancestors of the American fauna crossed the Bering bridge in late Tertiary. Rumpp (1961) considered that the ancestors of *C. willistoni* had already reached North America by the beginning of the Tertiary, and that there has been little evolution of this species since Miocene time. Freitag (1965) thought that the ancestral stock of *Cicindela* s. s. may have been in existence in early Tertiary, and that living species may have evolved during late Tertiary or early Pleistocene. Thus it is possible that the evolution shown in Figure 96 took place in

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[4] The question of land bridges is a touchy one. The presence of the Bering bridge during certain periods of geological time has been well established. Some early biogeographers were prone to "build" bridges where there was not the slightest shred of geological evidence to support them. For many years the trend has been away from this extreme. A related and even more volatile subject is continental drift. See Darlington (1957, 1965) and Simpson (1965) for recent discussions of these topics from the zoogeographical viewpoint.

late Mesozoic and early Cenozoic times. The Bering land bridge was uplifted during most of this time, and the climate at that latitude was mild (Miskimen, 1961).

SUBSPECIES

There has been a recent revival of interest in the question of whether subspecies have any reality in nature and, if so, whether they should be named in the formal system of Linnean nomenclature. Of particular importance is a series of papers in the journal, *Systematic Zoology.* Wilson and Brown (1953) condemned the arbitrariness and subjectivity of naming subspecies and pointed out several difficulties: 1) the tendency for independent characters to show independent geographic variation: 2) the ability of characters to appear in more than one geographic area, producing "polytopic" races; 3) the occurrence of microgeographic races; and 4) the necessary arbitrary lower limit of distinction of the subspecies. They further stated that subspecies as currently used are not units of evolution and that naming them conceals much variation. Other papers followed, supporting (Mayr, 1954; Parkes, 1955; Durrant, 1955; Smith and White, 1956) or refuting (Hubbell, 1959; Edwards, 1954; Peters et al., 1954; Gosline, 1954; Gillham, 1956; Hagmeier, 1958; Christiansen, 1958; Pimentel, 1959; Owen, 1963) the naming of subspecies.

My feelings on the subject, tempered by many of the above papers, as well as others, are as follows. Most of the difficulties mentioned by the opponents of subspecies are due to the extreme variability of animals. Populations of animals exist today in all stages of evolution, from a small, specifically distinct population inhabiting a single island, mountaintop, or valley, to widely distributed species, some of whose populations are not capable of interbreeding (see Mayr, 1963, for examples). In some species, one can find populations or groups of populations which are quite "distinct" in one or more characters from other populations of the species, while in other species this cannot be done. Thus, "distinct" intraspecific groups *may* exist within species. In the past, many such "distinct" groups (and some not so distinct) have been named as subspecies. At least some such groups (but by no means all) seem worthy of being named, if for no other reason than convenience in referring to them. In groups in which formal names have already been applied, one might just as well retain them. If no names exist, one may wish instead to use locality names or symbols to refer to them, as suggested by Hubbell (1954); although this may lead to confusion, as pointed out by Smith and White (1956). In some cases, some subspecies do appear to be units of evolution, as in geographically isolated populations, while in other cases they are not (at present), as in "distinct" groups among which gene flow occurs or is possible. There are all degrees of "distinctness" among intraspecific groups, making it impossible to set a nonarbitrary "lower limit" for subspecies. Statistical methods are useful in defining distinctness, but they can be misused. It is possible to find statistically "significant" differences between almost any two conspecific populations by using a large enough sample size, but these differences may have no biological significance. The many arbitrary limits, such as the "75% rule," the "84% rule," or the "95% rule," have been used with only limited success, and any one "rule" does not work well with all phyla of animals. Sokal and Rinkel (1963) pointed out the inadvisability of using such rules. I think that statistical methods, *plus* the opinion of a systematist familiar with the group of animals, are the only practical way to decide if a species should be subdivided and how, at our present state of knowledge. The recent development of methods such as numerical taxonomy may change this situation in the future.

Usually the naming of subspecies *does* conceal much variation; the study of species should not stop here. The variation of species, geographic and temporal, should be measured, studied, and shown by maps, graphs, etc. The use of a system of categories with a "higher degree of resolution," such as natio, subspecies, prospecies, species, and superspecies (see Schilder, 1953b, for an example using *Cicindela*), has not been popular, and in many cases the assignment of a form to a particular category is quite arbitrary. Subspecies are necessarily an oversimplification of the "true" situation. Nevertheless, if subspecies reflect to some degree the actual pattern of variation, as well as being convenient "handles" for reference, their value seems sufficient to justify their recognition.

In the genus *Cicindela* many of the species exhibit pronounced geographic variation, particularly of color and elytral maculation. For example, of the approximately 80 species occurring in North America north of Mexico, about 45 exhibit pronounced variation. Past workers have named many forms, which are now recognized as subspecies, varieties, intergrades, melanic forms, seasonal forms, and individual variants. Often, forms were described before the total distribution of variation of the species was known, or were described from inadequate series. Thus, one task of the present-day student of North American cicindelids is to make thorough studies of the variation of species and decide whether subspecies or formerly unrecognized sibling species exist (and should be named) within what have been called species. This will be done with the seven species studied thoroughly here.

Being familiar with the variation of many of the Cicindelas of North America, I think a subspecies in this group should have the following characteristics: (1) occupy a well defined geographic area or ecological habitat, separate from that of other subspecies within the same species (zones of intergradation may occur between neighboring subspecies); (2) exhibit a

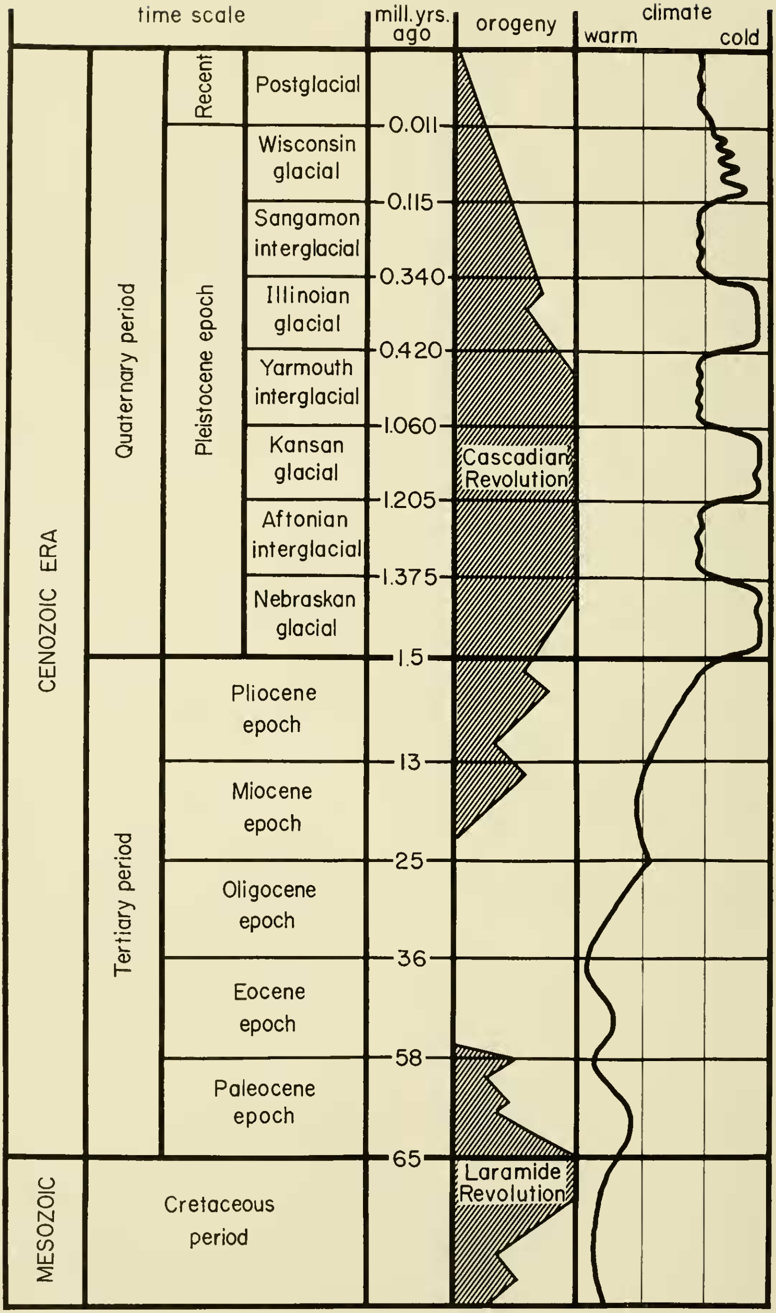

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FIG. 97. Partial geological time scale and important events in North America. From Dunbar (1960) and Dorf (1960).

relatively uniform expression of characters within itself; (3) be readily separable from other subspecies by one and preferably more characters.

These characteristics are obviously vague and contain no minimum degree of difference for a form to be a subspecies. I think each case should be considered individually (but comparison with the variational pattern of other species may be helpful) because cases will no doubt be found in which two forms may be "on the verge" of becoming species. Any clues on the past distribution or dispersal of the species (e.g., ancient river courses for fluvial species) should be considered. The problem is further complicated by the existence in many species of some forms which are much more distinct (and obviously subspecies) than others. Clearly there must be some subjectivity in the naming of subspecies.

CENOZOIC GEOLOGY AND CLIMATE

Before discussing the zoogeography of individual species, it would be well to review the major geological changes and paleoclimates that occurred in North America during the Cenozoic Era, when most of the evolution and dispersal of the species in this study probably took place. This amount is drawn from a number of sources. See Miller (1952), Dunbar (1960), King (1958), MacGinitie (1958), Dorf (1960), Braun (1947, 1955), Axlerod (1950), Chaney (1947), Deevey (1949), Dillon (1956), Thornbury (1965), and Wright and Frey (1965) for more details. See also Figure 97 for a geologic time scale.

The Cenozoic Era was marked by two great periods of orogeny, or mountain building activity. Beginning in the Cretaceous and continuing until early Eocene, the Laramide Revolution thrust up the initial Rocky Mountains in western North America. These mountains were eroded almost to a level peneplain by Miocene times, when the Cascadian or Cordilleran Revolution began, uplifting the western mountains again to their present height. During the Laramide Revolution, numerous basins were formed in the western United States, and in the Miocene, the Basin and Range province, which had a high mountainous surface and exterior drainage, began to assume its present character. As the initial Rockies were eroded, these basins were filled and sediment was carried eastward across the interior of the continent.

During most of the Tertiary, eastern North America, from central Alabama to the Gulf of St. Lawrence, which had been uplifted slightly at the close of the Cretaceous, was eroded to a nearly flat peneplain. Near the end of the Tertiary the area was again uplifted unevenly, and erosion increased to produce the present topography. The Atlantic and Gulf coastal plains were partially submerged from Paleocene to Oligocene or even Pliocene in some areas, but in general they gradually grew in size throughout the

Tertiary. A remnant from Cretaceous times, the Mississippi embayment, an arm of the Gulf of Mexico extending up the present Mississippi valley to southern Illinois, was gradually filled with sediment in the late Tertiary.

In late Cretaceous times, the climate was mild throughout most of the earth. Plants such as figs, cycads, palms, and tree ferns grew as far north as central Greenland and Alaska. The climate was nevertheless zoned as it is today. The tropics extended northward to about 35 or 40° latitude. From here to about 55 or 60° N latitude, subtropical conditions prevailed. Temperate climates extended to about 70° N latitude, north of which subarctic conditions occurred.

Conditions during the early Tertiary did not change greatly. The western mountains were mostly of moderate elevation and did not affect climate appreciably. By mid-Eocene times there were at least three botanical provinces in North America. In the far western states a subtropical forest extended along the coast and inland as far as northwestern Wyoming (Neotropical-Tertiary flora). The low-lying shores of the Mississippi embayment were occupied by a tropical flora (Wilcox flora). Far to the north extended the hardwood deciduous and coniferous Arcto-Tertiary forests. Arid conditions began to appear locally in northwestern Colorado and southern Wyoming, although the modern desert vegetation had not yet evolved.

Beginning in the Oligocene, a trend of gradual cooling and drying climates began. The northern Arcto-Tertiary forests began to move southward through the western United States, displacing tropical and subtropical floras. A climatic barrier of reduced rainfall prevented any of these species from entering the Appalachian region or Mexico. The Miocene saw the evolution of the semiarid Madro-Tertiary flora in northern Mexico and southern California, while the Arcto-Tertiary flora became more restricted. An ecotone existed between them in southern Nevada. The Arcto-Tertiary flora evidently still had a dispersal path to the eastern United States through southern Canada. In the vicinity of Washington, D.C., a low coast existed, lined with cypress swamps and coastal sand dunes.

Beginning in mid-Miocene and especially during the Pliocene, the present grasslands developed in the western two-thirds of the continent, replacing subtropical scrub in the region between the Rocky Mountains and the Mississippi embayment. Farther east, the mixed deciduous forests retreated and were replaced by oak forests. Temperatures cooled, rainfall decreased, and seasonal fluctuations increased, until in late Pliocene conditions were essentially like they are today. The uplift of the western mountains and their resultant rain-shadow effect played a major role in the development of the prairies and deserts.

The climatic changes begun in the Tertiary culminated in the Pleistocene epoch. A cyclic climatic pattern developed, producing alternating glacial and nonglacial stages. Four major glacial periods (the Wisconsin is subdivided by some authors) alternated with interglacials (Fig. 97). During the glacials, huge masses of ice moved southward, and mountain glaciers developed and increased in size. South of the glaciers rainfall increased, creating many large lakes in the Great Basin (the glacials are also called pluvial periods). The continental glaciers pushed farthest south in the central United States, reaching the present Ohio River and northeastern Kansas. Climatic zones were greatly compressed near the glaciers and shifted south (or down mountains) a certain amount; exactly how far is a point of disagreement among authors. Early authors thought that glaciation pushed the flora and fauna far south into Mexico and Central America. More recent authors, e.g., Dillon (1956), Dorf (1960), felt that climatic zones were more compressed than shifted south, and that the Gulf coast was still subtropical. Graham (1964) thought the glaciers had little effect on the biota of the southeastern United States. Probably a narrow band of tundra existed immediately south of the glaciers, followed by bands of subarctic, temperate, and subtropical climate as one moved south. Ranges of mountains in the West would produce a more complicated pattern, greatly influenced by elevation. During the interglacial periods the climatic zones and biota moved northward (and up mountains) to or slightly beyond their present positions.

The glaciers had profound effects on the sea level. During glacials the sea level was about 100 meters lower than at present, exposing much of the continental shelves and allowing the Bering land bridge to connect Eurasia and North America. The glaciers also had great effects on many North American streams. As mentioned, during glacials rainfall increased near the glaciers. Many streams in the Great Basin which now are intermittent or dry could have been important in the dispersal of certain organisms. Also, many changes in the courses of streams occurred and may have affected the distribution of organisms.

At present we appear to be in an interglacial period, with the next glacial period predicted to occur in 10,000 to 15,000 years. During the last several hundred years the mean world temperatures have been rising, glaciers are melting, and northward movements of animals such as seals, codfish, and armadillos have been noted.

MINOR SPECIES

Miscellaneous distribution records on the species not studied intensely follow.

C. duodecimguttata

The systematics and zoogeography of this species were studied thoroughly by Freitag (1965). Besides what has been mentioned in earlier sections, I offer the following personal collection records:

KANSAS: Republic Co., ½ mi. east, 1 mi. south of Talmo, 6 Sept. 1963; 4 mi. northwest of Jamestown, 14 Sept. 1964; Lincoln Co., 3 mi. west, 2 mi. south of Barnard, 14 Apr., 7 Sept. 1963; Greenwood Co., 2 mi. west, 1 mi. north of Severy, 11 May 1963; 1.5 mi. west of Severy, 11 May 1963; Wilson Co., west edge of Fredonia (city park), 11 May 1963, 6 Apr., 20 June 1964; Woodson Co., 5 mi. north of Yates Center, 20 Apr., 10 May 1963, 6 Apr. 1964; Butler Co., west edge of El Dorado, 11 July, 9 Sept. 1964, 21 May 1965; Sumner Co., 4.5 mi. west of Geuda Springs, 21 Apr. 1963; MISSOURI: Howard Co., 1 mi. north of Rocheport, 24 June 1963; TEXAS: Rockwall Co., 2.5 mi. southwest of Royse City, 30 June 1965.

C. hirticollis

This species is currently being studied by Dr. R. C. Graves. Collection records from saline habitats of the central United States are as follows:

KANSAS: Lincoln Co., 11 mi. north, ½ mi. east of Lincoln, 14 June 1964; Stafford Co., 11 mi. northeast of Hudson, 7 Apr. 1965; Barber Co., 3 mi. southeast of Hazelton, 27 Aug. 1963; 17.5 mi. west, 4 mi. north of Hardtner, 30 Aug. 1963; Comanche Co., 12 mi. south of Protection, 29 Aug. 1963; OKLAHOMA: Hughes Co., 5 mi. north of Holdenville, 29 June 1965; Seminole Co., 12.5 mi. south of Seminole, 29 June 1965; McClain Co., south edge of Purcell, 1 July 1965; Logan Co., 3 mi. north of Guthrie, 1 July 1965; Creek Co., just north of Oilton, 19 Aug. 1964; Woods Co., 2.5 mi. southwest of Plainview, 3 June 1963; Woods-Harper Co. line, 6 mi. west-northwest of Plainview, 29 Aug. 1963; Grant Co., just east of Pondcreek, 10 Sept. 1964; Major Co., 2 mi. northeast of Orienta, 12 July 1964; Kingfisher Co., 2 mi. south of Dover, 10 Sept. 1964; Blaine Co., 7 mi. south of Okeene, 21 June, 10 Sept. 1964; TEXAS: Cooke Co., 1 mi. northeast of Rosston, 30 June 1965.

Populations of *C. hirticollis* in the central United States have traditionally been called the subspecies *C. h. ponderosa* Thomson, but this is not satisfactory because the type locality is Veracruz, Mexico, and specimens from the two areas are not the same. The study by Graves should clarify the matter.

C. punctulata

This is an extremely common species which is found from central Mexico to southern Canada, and from Utah and Arizona to Maine and Florida. Most of the Mexican populations belong to the subspecies *C. p. catharinae* Chevrolat (see Cazier, 1954). In the southwestern United States is found the bright green, blue, or purple form, *C. p. chihuahuae* Bates. In general, the form east of the Rocky Mountains is the dark *C. p. punctulata* Olivier, although populations from Colorado, northeastern Utah, western Kansas, the Oklahoma and Texas panhandles, and eastern New Mexico seem to be intergrades between *C. p. punctulata* and *C. p. chihuahuae.* Collection records from this study (county only) are as follows:

NEBRASKA: Lancaster, Saunders; KANSAS: Republic, Lincoln, Mitchell, Russell, Neosho, Greenwood, Woodson, Wilson, Montgomery, Butler, Sedgwick, Sumner, Stafford, Kingman, Kiowa, Barber, Comanche, Clark; MISSOURI: Howard; OKLAHOMA: Seminole, Logan, Creek, Osage-Pawnee Co. line, Woods, Alfalfa, Grant, Major, Garfield, Blaine, Kingfisher, Beckham, Harmon; TEXAS: Fannin, Hunt, Collin, Montague.

C. repanda

This widely distributed species occurs from Texas (and possibly Mexico, near El Paso, Texas) to about 58° N latitude in Canada, and from Washington to Nova Scotia (it is absent from the Great Basin but occurs on the Colorado Plateau). It exhibits little geographic variation. Populations in Nova Scotia and vicinity have reduced elytral maculation and have been designated *C. r. novascotiae* Vaurie. Individuals in east central Utah are small, with expanded elytral maculation, and are called *C. r. tanneri* Knaus. The remaining populations may be called *C. r. repanda* Dejean, although other names have been applied to certain forms. Collection records from saline habitats are as follows (county only):

NEBRASKA: Saunders; KANSAS: Republic, Lincoln, Russell, Wilson, Sumner, Kiowa, Barber, Comanche; MISSOURI: Howard; OKLAHOMA: Hughes, Seminole, McClain, Creek, Woods, Alfalfa, Grant, Garfield, Kingfisher; TEXAS: Cooke.

C. schauppi

This is a species of southern distribution which reaches its northern limit in the central United States. North of Texas it is uncommon. I have collected it only once, in Okfuskee Co., Oklahoma, just northwest of Pharoah (19 Aug. 1964), on a bare, slightly saline area caused by oil drilling. This and other localities from the literature and museum collections are shown in Figure 98. *C. schauppi* exhibits some variation, specimens from northern localities having a longer, thinner, and more oblique middle band than do those from

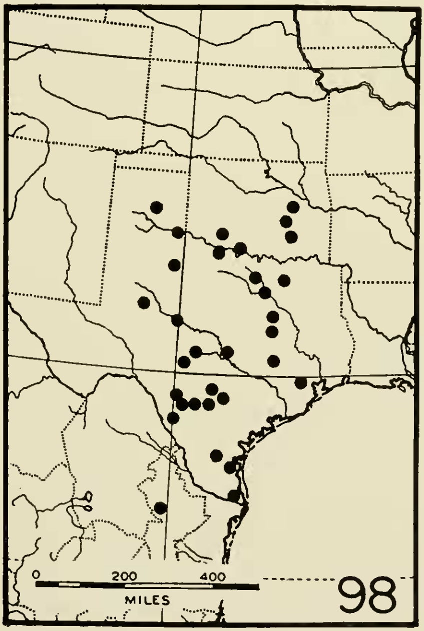


Fig. 98. Known distribution of *C. schauppi*. Fig. 99. Known distribution of *C. circumpicta*; triangle=*C. c. circumpicta*, dot=*C. c. johnsoni*.

southern and western Texas, but so few large series of specimens exist that a statistical study of variation would not be very meaningful. Further study may show that subspecies are worthwhile naming. Locality records are as follows (county or state only):

OKLAHOMA: Okfuskee, Coal, Hughes, Jefferson, Comanche; TEXAS: Wichita, Hunt, Wilson, Atacosa, Brazos, Frio, Uvalde, Limestone, King, Dimmet, Cameron, Kleberg, Burnet, Dallas, Childress, Kimble, Zavala, Bexar, Mason, Runnels, Duval, Denton, Nevarro, Nueces, Howard, Carson, Harris; MEXICO: Nuevo Leon. Doubtful locality: KANSAS: Parsons, Labette Co.; this specimen more resembles those from southern Texas than those from Oklahoma.

C. tranquebarica

This is a very widely distributed species, found from the Pacific coast to Newfoundland and from the Gulf coast to 60° N latitude in Canada. Populations east of the Rocky Mountains exhibit little variation and are called *C. t. tranquebarica* Herbst. West of the Rocky Mountains there occurs a multitude of subspecies (at least 11), which have been insufficiently studied. Collection records for saline habitats are the following:

KANSAS: Republic Co., 4 mi. west, 1 mi. south of Kackley, 6 Sept. 1963; Stafford Co., 11 mi. northeast of Hudson, 9 Apr. 1964; OKLAHOMA: Woods Co., 2.5 mi. southwest of Plainview, 3 June 1963.

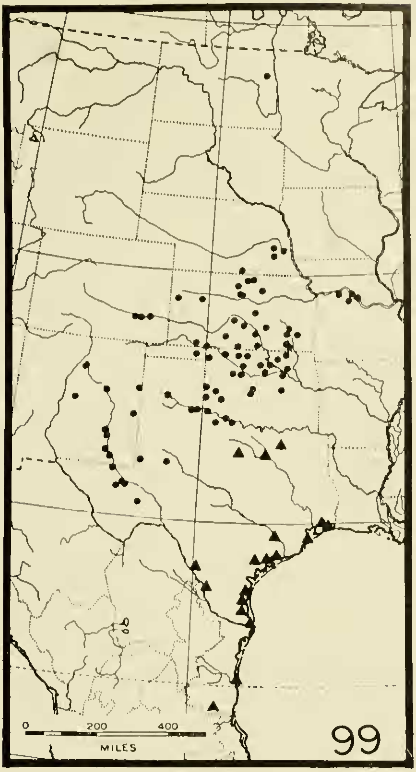
MAJOR SPECIES

In this section, those species that were studied most thoroughly are discussed. For each species, I will consider: (1) present distribution (as well as it is known), geographic variation, and the presence or absence of subspecies; (2) why it is found where it is, including adaptations, evolution, and dispersal.

C. circumpicta

This species is of primarily southern distribution, being most common along the western Gulf coast, along the Pecos River, and in Oklahoma and Kansas. It also occurs in Colorado, Missouri, Nebraska, and has recently been collected in eastern North Dakota (Fig. 99). *Doubtful records* exist (Lyons, Cook Co., Illinois; Riley Co., Kansas; Patagonia, Santa Cruz Co., Arizona); and the town of Manzenda, Colorado (=Manzanola, Otero Co. ?) could not be located. Locality records are as follows (county or state only):

NORTH DAKOTA: Grand Forks; NEBRASKA: Lancaster, Nuckolls, Saunders; MISSOURI: Boone, Howard, Saline; KANSAS: Barber, Butler, Clark, Clay, Gove, Kiowa, Lincoln, McPherson, Meade, Mitchell, Montgomery, Neosho, Reno, Republic, Sedgwick, Seward, Stafford, Sumner, Wallace, Wilson, Woodson; COLORADO: Bent, Otero; OKLAHOMA: Alfalfa, Beaver, Beckham, Blaine, Cleveland, Creek, Garfield, Grant, Harmon, Harper, Jackson, Kingfisher, McClain, Noble, Okfuskee, Oklahoma, Osage, Pawnee, Payne, Tillman, Tulsa, Washington, Woods; NEW MEXICO: Chaves, Eddy, Guadalupe, Quay, Roosevelt, Santa Fe, Torrance; TEXAS: Andrews, Cameron, Childress, Colorado, Dallas, Dimmet, Galveston, Goliad, Hall, Hardeman, Howard, Hunt, Jackson, Jefferson, Kenedy, Kleberg, Loving, Nueces, Palo Pinto, Pecos, Randall, Reeves, Victoria, Webb, Wichita, Wilbarger; TAMAULIPAS.

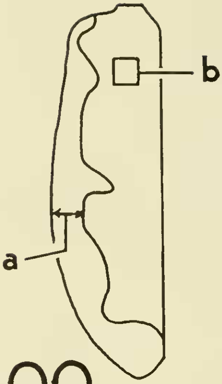


The described forms within this species are the following:

Cicindela circumpicta LaFerté, 1841. Type locality: Texas.
Cicindela collaris LaFerté, 1841. Type locality: Texas.
Cicindela Johnsonii Fitch, 1856. Type locality: prairies west of Arkansas.
Cicindela circumpicta ambiens Casey, 1913. Type locality: Kansas.
Cicindela circumpicta inspiciens Casey, 1913. Type locality: Point Isabel, Texas.
Cicindela circumpicta salinae Vaurie, 1951. Type locality: Lincoln, Lancaster County, Nebraska.

In recent years, three subspecies have been recognized: *C. c. circumpicta*, the dark, mostly coastal form; *C. c. johnsoni*, the bright inland form occurring in three color phases; and *C. c. salinae*, the dull reddish or brown form from the Lincoln, Nebraska, vicinity.

In the study of geographic variation, the following characters were measured: (1) width of head at widest point (the eyes); (2) width of pronotum at widest point; (3) width of left elytron at widest point when viewed from directly above, not at an oblique lateral angle; (4) width of the white elytral maculation at a specified place (Fig. 100a); (5) length of left elytron from the level of the anterior end of the scutellum to the most apical part; (6) num-



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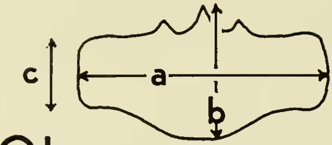

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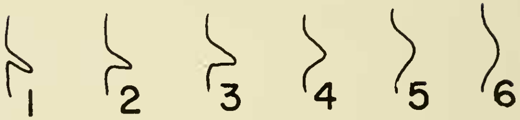

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FIGS. 100-102. Illustration of certain characters measured on *C. circumpicta*; FIG. 100, a=width of elytral maculation, b=number of punctures in 0.45 mm^2 area at this position; FIG. 101, a=width of labrum, b=length of labrum, c=length of labrum at one lateral edge; FIG. 102, arbitrary units for shapes of the middle bands.

ber of punctures in a 0.45 mm^2 square on a specified part of the left elytron (Fig. 100b); (7) width of labrum at widest point (Fig. 101a); (8) length of labrum at midline, including tooth (Fig. 101b); (9) length of labrum at one lateral edge (Fig. 101c); (10) length of hind tarsus, excluding claws; (11) length of hind tibia; (12) shape of middle band in arbitrary units (Fig. 102); (13) color of elytra, using color wheel.

Specimens from 23 localities were measured for characters 1-12; the localities and sample sizes are given in Table 13. Specimens from 21 of these localities and ten additional localities were included in the color analysis (Table 13). When possible, samples of 20 specimens of each sex were used, but in a few cases only small samples were available or specimens from two or more nearby localities were lumped into a larger sample. The values obtained from these less desirable samples are thus less reliable than those of samples from one locality.

The means for the characters and localities are given in Tables 14 and 15. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 16 and 17. The sums of the among-locality variance components are 100.907 for males and 127.336 for females. The first six components for males and the first seven for females are highly significant ($p < 0.01$), and the seventh is significant at the 5% level for males; however, the first three functions account for 77.67% of the variance (among localities relative to that within) in males and 78.19% in females. The first six functions account for 93.96%

TABLE 13. Localities and samples sizes of the specimens of *C. circumpicta* measured.

		N	
	Locality	♂	♀
1.	NORTH DAKOTA, Grand Forks Co., 1.5 mi. n.e. of Emerado	20	20
2.	NEBRASKA, Lancaster Co., Lincoln (west edge)	20	20
3.	KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	9	14
4.	KANSAS, Republic Co., 4 mi. w., 1 s. of Kackley	20	15
5.	KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	20	20
6.	KANSAS, Stafford Co., 11 mi. n.e. of Hudson	20	20
7.	MISSOURI, Howard Co., 1 mi. n., 2 w. of Boonesboro	20	20
8.	KANSAS, Montgomery Co., 3 mi. s. of Elk City	20	20
9.	OKLAHOMA, Creek Co., 3 mi. s.e. of Sapulpa	20	19
10.	OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	20	20
11.	OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	20	20
12.	KANSAS, Clark Co., Englewood	20	20
13.	OKLAHOMA, Blaine Co., 7 mi. s. of Okeene	17	10
14.	OKLAHOMA, Beckham Co., 6 mi. w. of Mayfield	14	11
15.	OKLAHOMA, Jackson Co., 3.5 mi. s. of Eldorado	20	17
16.	NEW MEXICO, Chaves Co., 10 mi. e., 5 s. of Roswell	20	20
17.	NEW MEXICO, Eddy Co., 6 mi. e., 2 n. of Loving	11	8
18.	TEXAS, Reeves Co., vicinity of Pecos, Lake Balmorhea, Toyah; Pecos, Co., Ft. Stockton; Loving Co.	13	20
19.	TEXAS, Webb Co., Laredo; Dimmet Co., Carrizo Springs	6	6
20.	TEXAS, Cameron Co., Port Isabel, Boca Chica, Brownsville	12	19
21.	TEXAS, Kleberg Co., Riviera Beach	20	20
22.	TEXAS, Galveston Co., Seabrook, Galveston, Dickinson*	1	2
23.	TEXAS, Dallas Co., Dallas; Hunt Co., Wolfe City*	2	3
Localities included in color analysis only:			
24.	KANSAS, Lincoln Co., 11 mi. n. of Lincoln		
25.	KANSAS, Wilson Co., 1 mi. n., ½ w. of Fredonia		
26.	KANSAS, Neosho Co., 2 mi. n., ½ e. of Chanute		
27.	KANSAS, Sumner Co., just n. of Geuda Springs		
28.	KANSAS, Barber Co., 3 mi. s.e. of Hazelton		
29.	KANSAS, Kiowa Co., 1 mi. n. of Belvidere		
30.	OKLAHOMA, Tulsa Co., 1.5 mi. s. of Skiatook		
31.	OKLAHOMA, Garfield Co., ½ mi. n.w. of Drummond		
32.	OKLAHOMA, Beckham Co., 3 mi. s. of Carter		
33.	TEXAS, Wichita Co., 2 mi. n.e. of Burkburnett		
34.	TEXAS, Hardin Co., Sour Lake		

* Excluded from color analysis.

TABLE 14. Means of 23 localities (see Table 13) and 12 characters for males of *C. circumpicta*. Values for characters 1-5, 7-11 are in mm.

	Character											
Locality	1	2	3	4	5	6	7	8	9	10	11	12
1	3.36	2.57	2.21	0.61	8.16	30.4	1.60	0.75	0.47	4.91	4.86	4.18
2	3.33	2.54	2.15	0.41	7.97	34.4	1.54	0.71	0.44	4.68	4.71	2.96
3	3.46	2.73	2.25	0.44	8.51	33.3	1.62	0.75	0.46	5.14	4.99	3.31
4	3.53	2.81	2.34	0.46	8.62	30.9	1.65	0.79	0.48	5.25	5.23	2.85
5	3.26	2.56	2.13	0.41	7.88	33.8	1.51	0.73	0.44	4.77	4.76	3.00
6	3.53	2.76	2.33	0.52	8.54	28.8	1.63	0.80	0.48	5.15	5.21	3.45
7	3.51	2.73	2.29	0.41	8.42	29.5	1.62	0.79	0.50	4.89	4.93	3.13
8	3.50	2.72	2.31	0.44	8.52	29.6	1.60	0.76	0.47	4.95	5.01	3.01
9	3.39	2.59	2.20	0.50	8.09	30.8	1.55	0.76	0.46	4.81	4.82	3.27
10	3.47	2.69	2.31	0.46	8.30	29.7	1.59	0.77	0.48	4.95	5.04	3.46
11	3.52	2.72	2.34	0.50	8.51	28.8	1.61	0.79	0.49	5.13	5.18	3.30
12	3.25	2.54	2.19	0.49	7.90	31.8	1.49	0.71	0.45	4.90	4.85	3.89
13	3.40	2.47	2.20	0.43	7.91	29.0	1.49	0.72	0.45	4.73	4.79	3.06
14	3.45	2.63	2.30	0.47	8.32	31.1	1.60	0.76	0.48	5.12	5.12	3.11
15	3.61	2.78	2.43	0.54	8.81	29.1	1.65	0.81	0.51	5.18	5.22	3.13
16	3.47	2.67	2.30	0.57	8.39	32.3	1.60	0.77	0.49	5.42	5.39	3.76
17	3.31	2.48	2.16	0.57	7.89	34.6	1.49	0.72	0.46	5.04	5.01	4.29
18	3.54	2.73	2.35	0.64	8.55	29.6	1.63	0.80	0.50	5.42	5.35	3.98
19	3.45	2.50	2.21	0.42	8.19	29.0	1.53	0.83	0.48	5.18	5.17	1.93
20	3.79	2.87	2.38	0.40	8.73	22.0	1.70	0.88	0.52	5.62	5.58	1.64
21	3.92	2.97	2.48	0.42	8.99	22.4	1.78	0.89	0.54	5.88	5.85	1.38
22	3.17	2.25	2.05	0.46	7.17	33.0	1.36	0.69	0.39	4.61	4.56	1.20
23	3.33	2.59	2.10	0.38	8.12	29.0	1.55	0.82	0.46	4.99	4.89	1.95

TABLE 15. Means of 23 localities (see Table 13) and 12 characters for females of *C. circumpicta*. Values for characters 1-5, 7-11 are in mm.

	Character											
Locality	1	2	3	4	5	6	7	8	9	10	11	12
1	3.66	2.83	2.44	0.55	8.62	27.7	1.71	0.80	0.47	4.28	4.73	4.02
2	3.72	2.90	2.44	0.47	8.72	31.1	1.69	0.80	0.47	4.37	4.79	2.98
3	3.72	2.91	2.49	0.47	8.91	31.1	1.70	0.79	0.48	4.49	4.88	2.89
4	3.75	3.01	2.55	0.49	9.04	28.6	1.74	0.82	0.48	4.51	4.87	2.97
5	3.51	2.73	2.34	0.41	8.41	30.1	1.61	0.75	0.46	4.28	4.66	3.09
6	3.85	3.02	2.59	0.48	9.12	26.5	1.75	0.85	0.52	4.58	5.06	3.06
7	3.70	2.84	2.41	0.40	8.74	28.1	1.70	0.82	0.51	4.26	4.75	3.13
8	3.75	2.90	2.47	0.45	8.88	27.2	1.71	0.80	0.49	4.41	4.85	3.16
9	3.68	2.82	2.40	0.51	8.70	28.5	1.65	0.81	0.47	4.32	4.66	3.11
10	3.74	2.88	2.50	0.43	8.94	28.3	1.70	0.81	0.49	4.46	4.93	3.35
11	3.77	2.92	2.56	0.46	8.97	27.2	1.71	0.82	0.51	4.57	5.05	3.22
12	3.53	2.77	2.40	0.50	8.42	28.0	1.61	0.76	0.47	4.38	4.78	3.38
13	3.74	2.88	2.53	0.45	8.90	29.8	1.70	0.83	0.51	4.43	4.91	2.89
14	3.78	2.90	2.51	0.47	8.98	28.5	1.72	0.81	0.50	4.57	4.97	3.01
15	3.91	3.06	2.65	0.57	9.32	27.4	1.76	0.86	0.53	4.66	5.10	3.24
16	3.69	2.87	2.48	0.56	8.79	30.3	1.66	0.80	0.50	4.60	5.07	3.74
17	3.53	2.65	2.31	0.52	8.38	34.4	1.53	0.75	0.47	4.34	4.69	3.83
18	3.89	2.99	2.60	0.63	9.13	29.3	1.76	0.86	0.53	4.76	5.32	3.48
19	3.58	2.62	2.37	0.39	8.65	26.2	1.57	0.85	0.50	4.39	4.86	1.13
20	4.11	3.08	2.58	0.39	9.14	22.2	1.79	0.91	0.53	4.99	5.45	1.33
21	4.20	3.20	2.65	0.39	9.46	21.5	1.87	0.96	0.57	5.22	5.70	1.32
22	3.51	2.61	2.33	0.38	8.27	26.5	1.54	0.82	0.47	4.35	4.84	1.60
23	3.60	2.73	2.34	0.43	8.33	24.7	1.58	0.78	0.45	4.28	4.74	1.13

TABLE 16. Pooled within-locality variance-covariance matrix for males of *C. circumpicta*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4} to conserve space; thus "253"=0.0253.

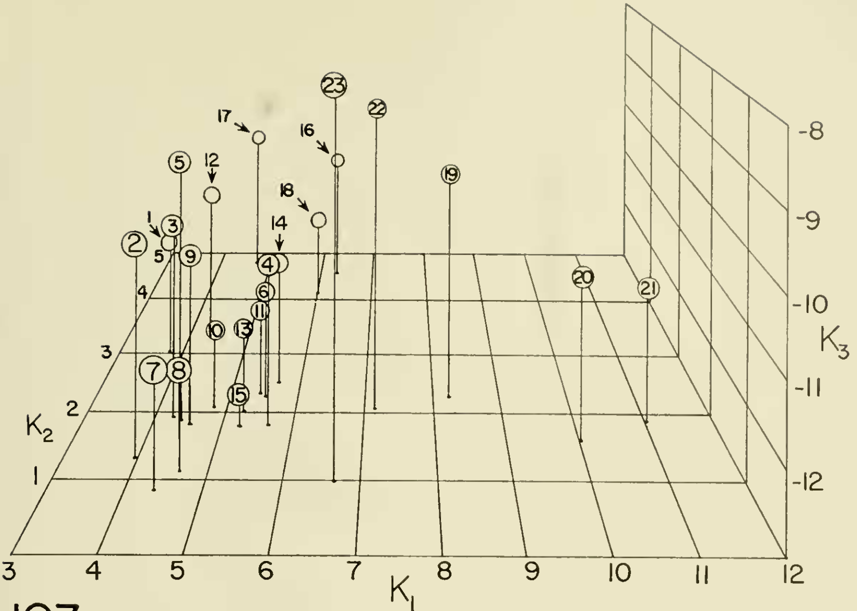
	Character											
Character	1	2	3	4	5	6	7	8	9	10	11	12
1	253	240	184	41	647	−1049	134	82	50	351	370	−38
2		394	304	62	1074	846	216	117	70	593	623	−86
3			284	64	908	983	176	97	60	504	528	−73
4				143	190	267	36	24	13	104	119	211
5					3503	2670	634	346	213	1864	1953	−259
6						141199	509	221	156	2148	2068	670
7							137	70	43	350	367	−33
8								49	25	191	198	2
9									19	120	125	−5
10										1256	1178	−69
11											1301	−49
12												4403

TABLE 17. Pooled within-locality variance-covariance matrix for females of *C. circumpicta*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4} to conserve space; thus "304"=0.0304.

Character	1	2	3	4	5	6	7	8	9	10	11	12
1	304	251	204	45	635	−2078	130	73	43	264	316	−106
2		258	187	40	567	−1950	117	66	39	244	285	−92
3			184	41	490	−1585	96	53	32	203	239	−95
4				63	98	−266	21	10	5	39	56	123
5					1767	−5664	308	179	104	663	815	−180
6						100873	−1039	−620	−343	−2390	−2543	97
7							72	37	22	133	157	−14
8								34	14	84	100	−23
9									12	47	56	−18
10										461	419	−68
11											607	17
12												3047

in males and 92.10% in females. The distributions of the means in the first three discriminant functions are shown in Figures 103 and 104. The localities fall into two loose clusters in both sexes, with localities 19-23 in one and all other localities in the other. The two clusters are not as widely separated in males as they are in females; however, there is still a distinct break between them because localities 19, 22, and 23 have high values in K_3, while the nearest localities in the other cluster have lower values. The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 6 vs. 11, 10 vs. 11, 19 vs. 22, and 22 vs. 23 for both sexes; 4 vs. 6, 11 vs. 14, 11 vs. 15, and 16 vs. 18 for males; and 2 vs. 3, 8 vs. 10, 11 vs. 13, 3 vs. 14, 6 vs. 14, 8 vs. 14, 10 vs. 14, 11 vs. 14, and 13 vs. 14 for females. Thus, several pairs within the clusters are not significantly different, but the nearest intercluster pairs are significantly different. Localities 16, 17, and 18 could be considered a subcluster; however, including samples from geographic areas between them and their nearest neighbors would probably destroy this appearance.

Sets of vectors (Figs. 105 and 106), plotted for the first two discriminant functions, show the geographic trends of the 12 characters when compared with Figures 103 and 104. Thus, specimens with high values in K_1 (the right-hand cluster) have high values for characters 1, 8, 10, and 11 and low values for characters 2, 3, 5, and 7; while specimens with low values in K_1 show the opposite trend (when all characters are considered simultaneously). Similarly, specimens high in K_2 are also high in characters 4 and 9, and low in 7 and 8.



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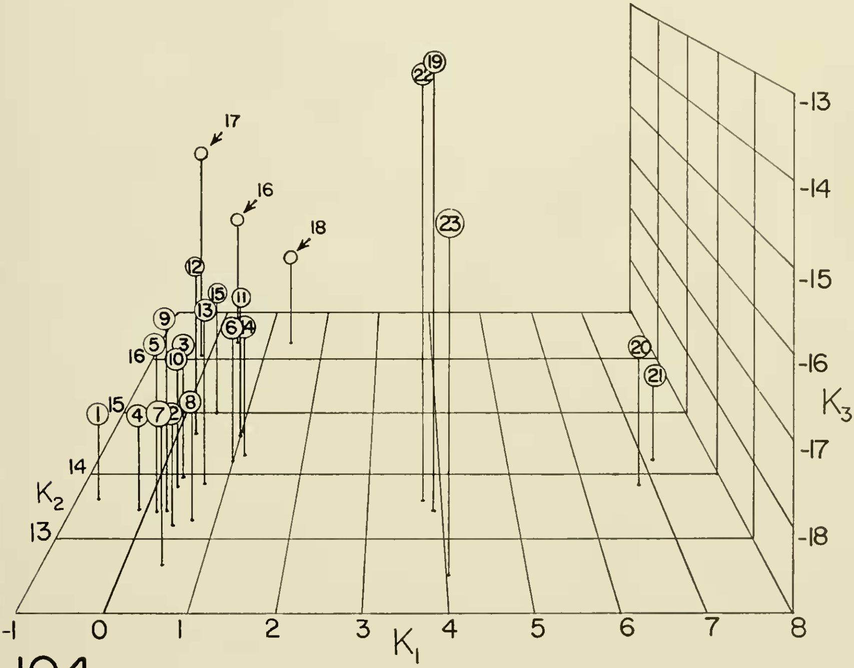
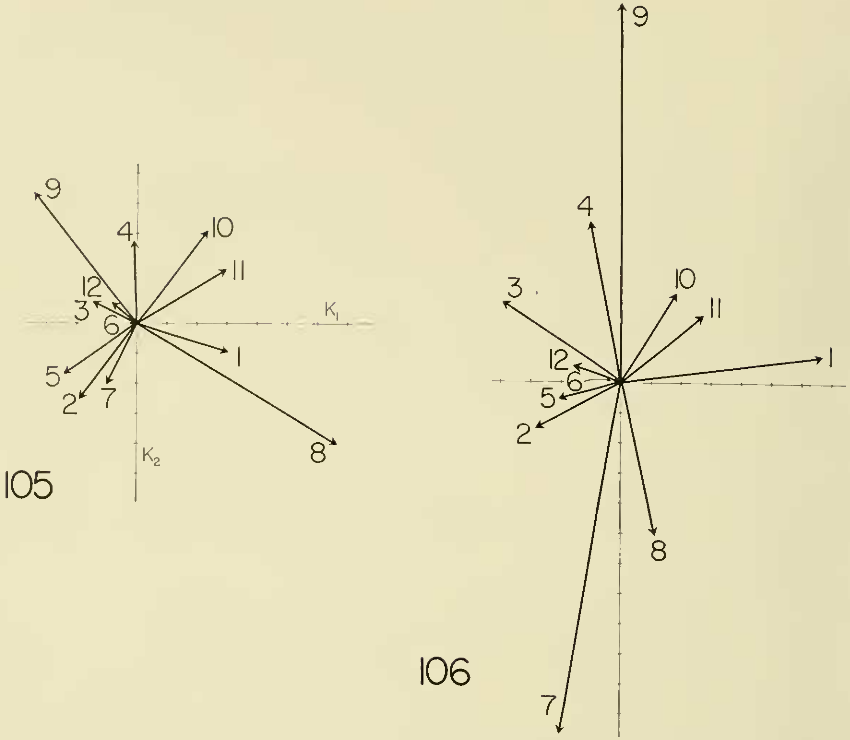


104

FIGS. 103-104. Distributions of the means of 23 localities for males (Fig. 103) and females (Fig. 104) of *C. circumpicta* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.



FIGS. 105-106. Vectors for the 12 characters of males (Fig. 105) and females (Fig. 106) of *C. circumpicta* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 103-104.

The results of the color analysis are shown in Figure 107. Populations from near the Gulf Coast and lower Rio Grande valley are nearly uniformly dark purplish to dark olive green, although in the vicinity of Corpus Christi, Texas, a small percentage of bright green, blue-green, and blue individuals occur. Most other populations contain individuals in bright reddish, green, and blue morphs in varying proportions. In general, reddish individuals are most common, followed by green and blue. In several scattered localities, reddish individuals compose nearly the entire population (southern New Mexico, southwestern and west-central Oklahoma, north-central Kansas, Nebraska, and North Dakota). In Missouri only blue to green individuals occur, while populations in southeastern Kansas and northeastern Oklahoma contain a higher percentage of these morphs than western populations. The southern-most sample in eastern Oklahoma contains an unusually high number of dark individuals. The North Dakota population is unique in containing about 15% black (or at least very dark purple) individuals. Thus, we

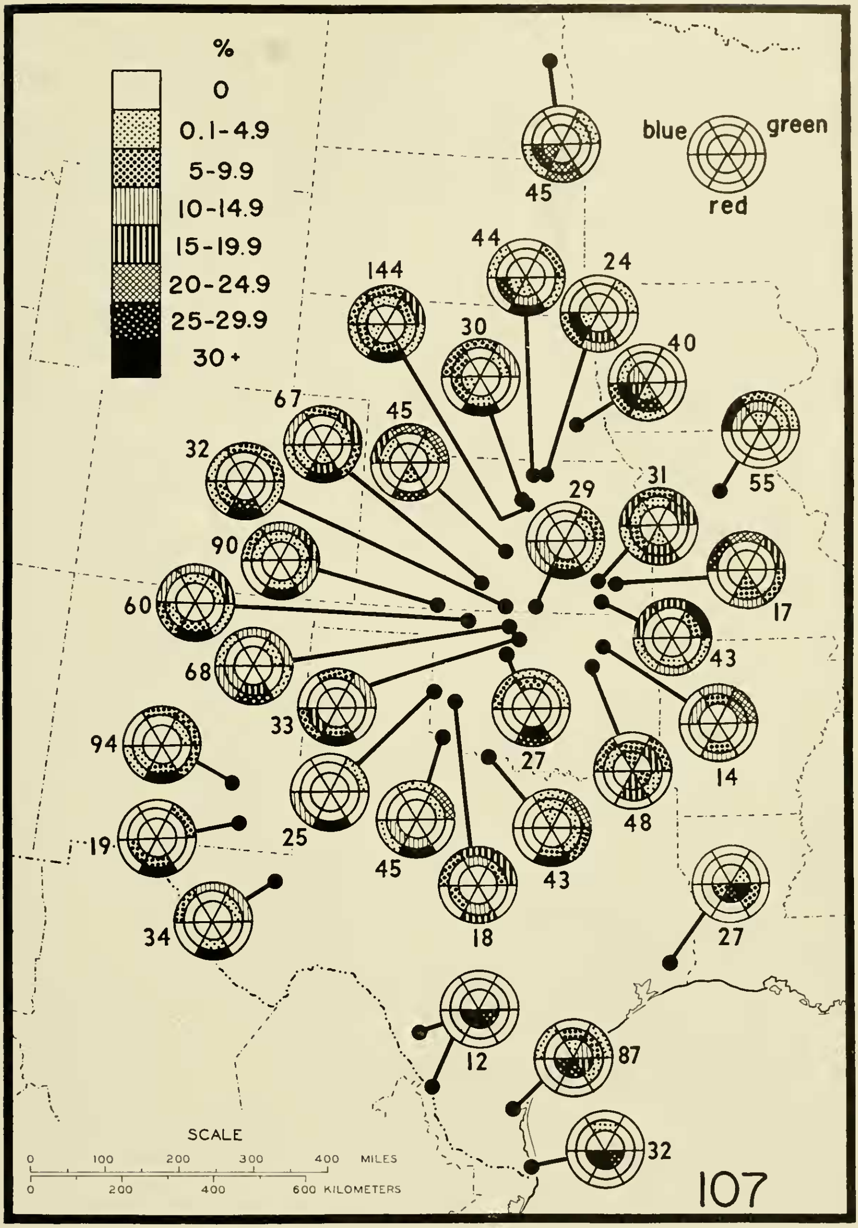


Fig. 107. Results of color analysis of *C. circumpicta* using the color wheel. Different degrees of shading indicate different percentages of the sample (upper left). The positions of the three major colors are shown at upper right. Numbers show the sample size for each locality.

may divide the samples into two major groups: the rather uniform dark coastal populations and the quite heterogeneous, usually bright inland populations, which exhibit much intra- and interpopulation variation.

Considering the pattern of geographic variation shown by this species, I think it is best to recognize only two subspecies (Fig. 99): 1) *C. c. circumpicta*, characterized by narrow maculation, particularly a thin middle band, a relatively long labrum and wide head, and usually dark color, ranging from dark purplish to dark olive green, with occasional bright blue or green individuals; 2) *C. c. johnsoni*, having wider maculation, particularly a wider, often broadly rounded middle band; relatively short labrum and narrow head, and usually bright color, ranging from reddish to green to blue, with occasional brown or black individuals.

The recently described *C. c. salinae* was separated because of its small size, dull (not glossy) elytra, and brown or dark red color, with no blue or green individuals. The present analysis shows that populations of quite small individuals occur in several scattered localities. Although it was not measured, relatively dull elytra seem to be characteristic of populations from northern Kansas, Missouri, Nebraska, and North Dakota. The tendency for local populations to contain only one color morph seems not to be uncommon in this species. Thus, *C. c. salinae* does not seem sufficiently distinct to warrent its continued recognition.

C. circumpicta probably arose within its present range. Its closest relatives, *C. praetextata* and *C. californica*, occur in the southwestern United States and western Mexico. It is proposed that a common ancestor to the three became widespread from Texas to California during the late Tertiary. The rising mountains of the Cascadian Revolution and the drier, cooler climate of this time separated the ancestral species into at least three groups, which evolved into the modern species. Probably while this was occurring, proto-*circumpicta*, had already begun to become differentiated into coastal and inland forms, possibly in the form of a cline along the Rio Grande valley. Drier climates of the Pleistocene then extinguished intermediate populations in the upper Rio Grande valley. The fluctuating sea level of the Pleistocene probably "encouraged" *C. c. circumpicta* to disperse up many of the Texas rivers; today relict populations exist in the Dallas vicinity and the lower Rio Grande valley. *C. c. johnsoni* had not dispersed to Nebraska or central Missouri by mid-Pleistocene because the Nebraskan and Kansan glaciers covered these areas (or if it had reached these areas, it was driven back or exterminated). As it dispersed northeastward from its place of origin, *C. c. johnsoni* became more and more unlike the original stock, producing the entirely blue or green populations of Missouri and the entirely reddish populations near Lincoln, Nebraska. Central Missouri was apparently reached via southeastern Kansas.

The occurrence of reddish, green, and blue color morphs seems to have been a characteristic of the ancestral species of *C. circumpicta*, *C. praetextata*, and *C. californica*, because they occur in all three modern species. Thus, it is proposed that the coastal *C. c. circumpicta* has nearly lost this primitive character, while most populations of *C. c. johnsoni* have retained it. The bright green and blue morphs would seem to be at a great disadvantage in being camouflaged, and evidence presented earlier supports this (see section on ecological relationships of the adult). The pattern of color variation (Fig. 107) shows that, except for populations in northern Kansas, those populations with the highest percentage of bright reddish individuals occur in those regions that possess very red soil derived from the Permian redbeds (Fig. 108). This suggests that the bright green and blue morphs are gradually being lost in these areas. As populations from these areas dispersed northward into Kansas, Nebraska, and North Dakota, they encounted darker soils. The high frequency of darker red and purplish individuals from these localities indicates that evolution has occurred to produce better camouflaged individuals. The high percentage of rather bright blue and green individuals in southeastern Kansas and Missouri is difficult to explain; soils in these areas are generally dark. Perhaps dark green and dark purplish of *C. c. circumpicta* match very well the dark soils prevalent in the areas where it occurs.

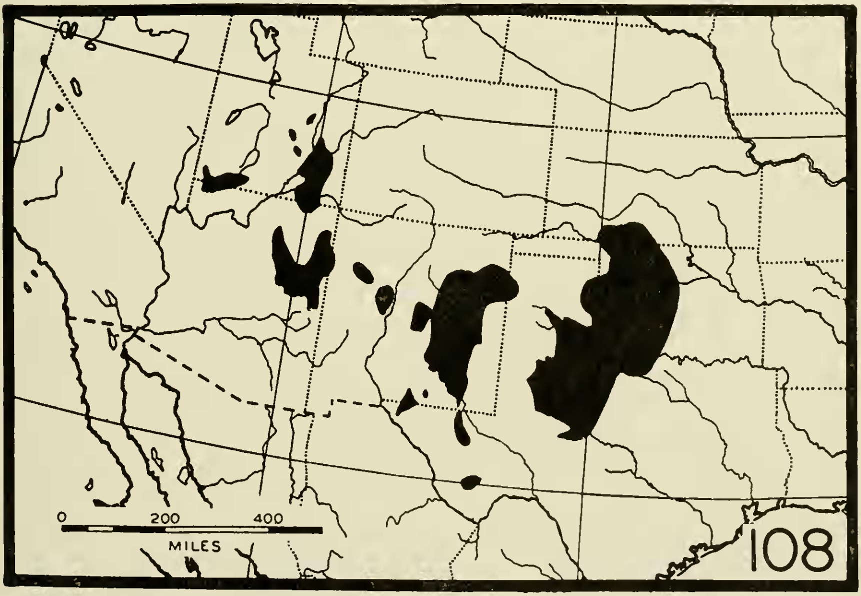


Fig. 108. Distribution of soils derived from the Permian redbeds. From map: Origin and distribution of United States soils, prepared by the Technical Development Service, Civil Aeronautics Administration and the Engineering Experimental Station, Purdue University (1946).

The wider markings of populations in southwestern Kansas, western Oklahoma, western Texas, and New Mexico seems to be an indirect result of the drier climate of these areas, which causes a white crust of salt to be present on saline habitats more of the time than in moister areas (see section on ecological relationships of the adult). The occurrence of widely maculate individuals in North Dakota seems to be a convergence that has taken place recently.

C. cuprascens

This species is most common between the Rocky and Appalachian Mountains (Fig. 109). The distribution by counties or states is the following:

GEORGIA; ALABAMA: Tuscaloosa; MISSISSIPPI: Warren; TENNESSEE: Shelby; KENTUCKY: Campbell, Fulton, Henderson, Kenton; OHIO; INDIANA: Posey, Putnam;

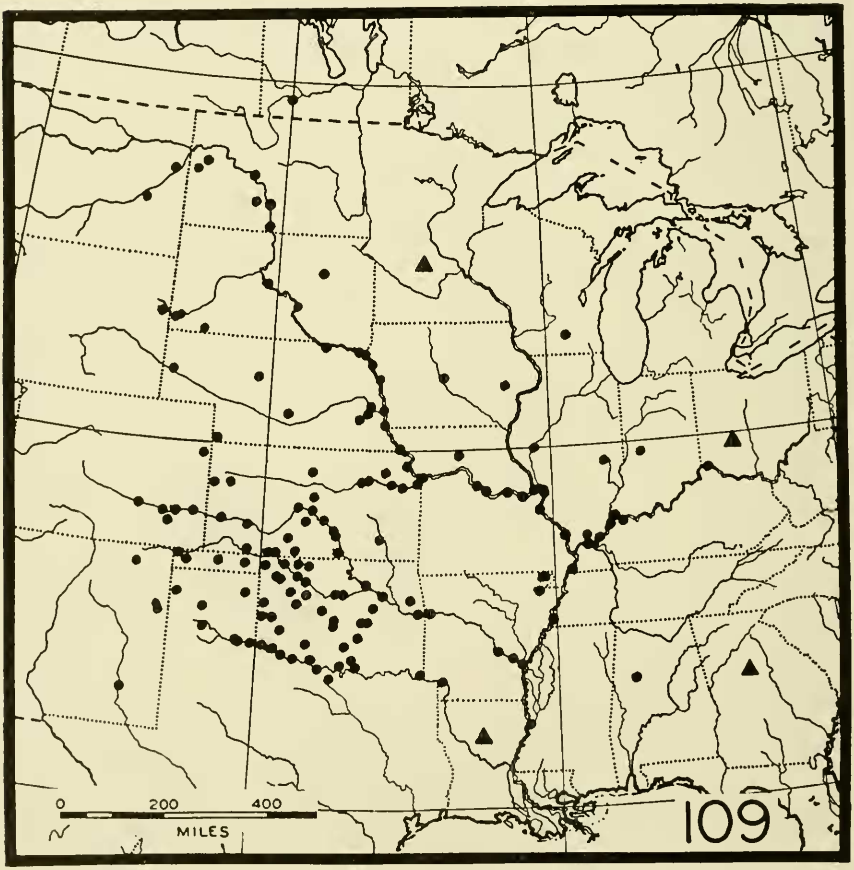


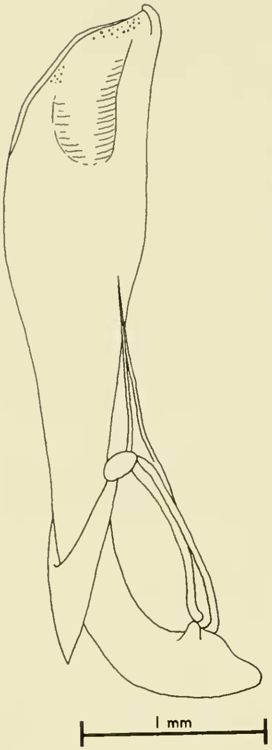
Fig. 109. Known distribution of *C. cuprascens*; triangle=state record.

ILLINOIS: Coles, Hardin, Jackson, Johnson, Masac, Morgan, Pope, Clair; WISCONSIN: Dane; MINNESOTA; IOWA: Johnson, Monona, Pottawatamie, Story, Woodbury; MISSOURI: Boone, Cooper, Franklin, Gasconade, Holt, Jefferson, Livingston, St. Charles, St. Louis; ARKANSAS: Arkansas, Clay, Craighead, Crawford, Desha, Jefferson, Lincoln, Miller, Sebastian; LOUISIANA; TEXAS: Childress, Cooke, Hall, Hardeman, Hartley, Hemphill, Hutchinson, Montague, Potter, Randall, Wichita, Wilbarger; OKLAHOMA: Alfalfa, Beaver, Beckham, Canadian, Cherokee, Cimarron, Cleveland, Comanche, Cotton, Custer, Dewey, Greer, Harper, Hughes, Jackson, Jefferson, Johnson, Kiowa, Logan, Love, Major, Marshall, McCurtain, Murray, Okfuskee, Payne, Pontotoc, Roger Mills, Sequoyah, Texas, Tillman, Tulsa, Woods, Woodward; KANSAS: Atchison, Barton, Clark, Clay, Douglas, Ellsworth, Finney, Ford, Gray, Hamilton, Johnson, Kearney, Kiowa, Leavenworth, Logan, McPherson, Meade, Pottawatomie, Reno, Rice, Riley, Sedgwick, Shawnee, Sumner, Wallace, Wyandotte; NEBRASKA: Buffalo, Cass, Dakota, Dixon, Douglas, Dundy, Knox, Otoe, Platte, Richardson, Scotts Bluff, Thomas; SOUTH DAKOTA: Brule, Clay, Fall River, Shannon, Spink, Union; NORTH DAKOTA: Billings, Burleigh, Emmons, Mc Kenzie, Mc Lean, Mercer, Morton; MANITOBA; MONTANA: Custer, Dawson; WYOMING: Niobrara; COLORADO: Bent, Denver, Otero, Prowers, Pueblo, Yuma; NEW MEXICO: Chaves, Colfax, Quay. Towns that could not be located: Eastport and Eastbrook, Iowa; Wicks, Missouri. Doubtful records: Moscow, Latah Co., Idaho; Logan Canyon, Cache Co.?, Utah.

A closely related form, which has been considered a subspecies of *C. cuprascens* (Horn, 1930; Leng, 1902), a subspecies of *C. macra* (Vaurie, 1951), or a separate species (G. Horn, 1876; Schaupp, 1883-1884), is *puritana* G. Horn. It is found along the Connecticut River in New Hampshire (Sullivan Co.), Massachusetts (Hampden and Hampshire Cos.), and Connecticut (Hartford Co.), and around Chesapeake Bay in Maryland (Calvert and St. Marys Cos.). State records exist for New York and Virginia. Some specimens appear to be labelled "Windsor, Can.," which is in southern Ontario. Wallis (1961) does not mention this record from Canada, and the labels probably should read "Windsor, Connecticut," where this form has been collected. After examining the adult morphology, including the male genitalia, I think *puritana* should be considered a separate species, one that is more closely related to *C. cuprascens* than to *C. macra*. The three species are compared in Table 18. In certain characters, *C. puritana* is somewhat intermediate between *C. cuprascens* and *C. macra*. Because of its distinct com-

TABLE 18. Comparison of seven characters in *C. cuprascens*, *C. puritana*, and *C. macra*.

Character	*C. cuprascens*	*C. puritana*	*C. macra*
Shape of posterio-lateral emargination of ♀ elytra	Acute	Acute	Rectangular
Shape of ♀ elytral apices	Rounded	Acute or occas. truncate	Acute
Depth of elytral punctation	Deep	Deep to shallow	Shallow
Elytral surface	Shiny	Shiny, occas. dull	Dull
Typical shape of apex of middle band	Globose or not enlarged	Globose or not enlarged	Recurved or triangular
Shape of aedeagus	More slender (Fig. 93)	Thicker (Fig. 110)	Thicker (Fig. 112)
Shape of tooth of inner sac	Long and acute (Fig. 95)	Long and acute (Fig. 111)	Shorter and blunt (Fig. 113)



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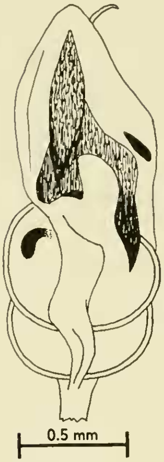

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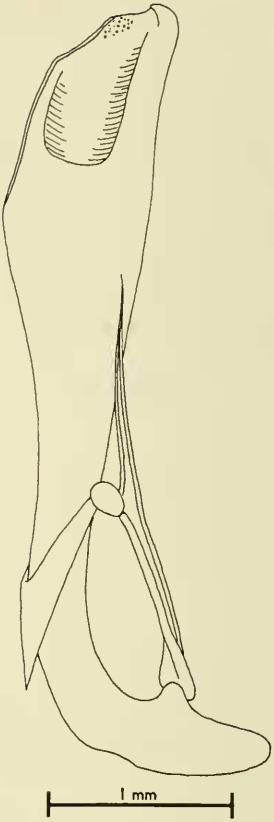

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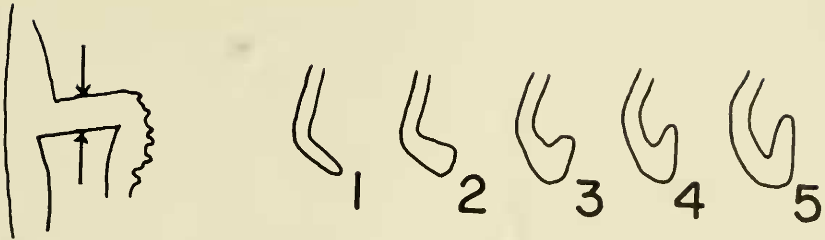
FIG. 110. Aedeagus of *C. puritana* (Windsor, Connecticut), dorsal aspect. FIG. 111. Inner sac of aedeagus of *C. puritana*, ventral aspect. FIG. 112. Aedeagus of *C. macra* (Ness County, Kansas), dorsal aspect. FIG. 113. Inner sac of aedeagus of *C. macra*, ventral aspect.

bination of characters, and because it is geographically isolated from *C. cuprascens* and *C. macra*, I have separated it taxonomically. As a test, it was included in the statistical analysis along with *C. cuprascens.*

In recent years, no subspecies have been recognized. The following forms have been described within the species *C. cuprascens*:

Cicindela cuprascens Leconte, 1852. Type locality: Arkansas River (types bear green paper circles, signifying "Kansas, Nebraska, and westward")
Cicindela cuprascens amnicola Casey, 1913. Type locality: Kentucky, Illinois, and Missouri.
Cicindela mundula Casey, 1913. Type locality: Vicksburg, Mississippi.

In the study of geographic variation, the following characters were measured : (1) length of left elytron; (2) width of left elytron; (3) width of



Figs. 114-115. Illustrations of certain characters measured on elytra of *C. cuprascens*, *C. puritana*, and *C. macra*; Fig. 114, width of middle band; Fig. 115, arbitrary units for shape of apex of middle band.

labrum; (4) length of labrum, including tooth; (5) width of middle band at a specified place (Fig. 114); (6) width of head; (7) shape of apex of middle band in arbitrary units (Fig. 115); (8) color of elytra, using color wheel.

Specimens from nine localities were measured; the localities and sample sizes are given in Table 19. Sample sizes were adequate from all the localities; however, specimens from several localities in Alabama and Missouri were lumped.

Table 19. Localities and sample sizes of the specimens of *Cu puritana* and *C. cuprascens* measured.

Locality	N ♂	N ♀
C. puritana:		
1. CONNECTICUT, Hartford Co., Windsor	12	12
C cuprascens:		
2. ALABAMA, Tuscaloosa Co., several localities	12	7
3. MISSOURI, St. Louis Co., St. Louis; St. Charles Co., St. Charles	12	12
4. IOWA, Pottawattamie Co., Council Bluffs	12	12
5. KANSAS, Douglas Co.	12	12
6. KANSAS, Clark Co., 8 mi. s. of Sitka	12	12
7. OKLAHOMA, Alfalfa Co., 3 mi. n., 5 e. of Cherokee	12	12
8. OKLAHOMA, Cleveland Co.	12	12
9. COLORADO, Bent Co., Las Animas	12	12

The means for the characters and localities are given in Tables 20 and 21. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes except character 2 for females, which is significant at the 5% level. Pooled within-locality variance-covariance matrices are given in Tables 22 and 23. The sums of the among-locality variance components are 82.768 for

TABLE 20. Means of nine localities (see Table 19) and seven characters for males of *C. puritana* and *C. cuprascens*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	7.32	2.01	1.39	0.64	0.31	2.84	1.54
2	6.73	1.89	1.34	0.59	0.27	2.62	2.67
3	7.16	1.90	1.41	0.63	0.30	2.90	2.06
4	7.46	2.00	1.47	0.63	0.36	2.91	2.43
5	7.38	1.92	1.44	0.63	0.34	2.91	2.22
6	7.79	2.04	1.56	0.70	0.46	3.15	2.50
7	7.46	2.02	1.53	0.68	0.43	3.08	2.21
8	7.46	2.02	1.51	0.66	0.43	3.05	2.54
9	7.57	2.03	1.54	0.66	0.45	3.00	2.96

TABLE 21. Means of nine localities (see Table 19) and seven characters for females of *C. puritana* and *C. cuprascens*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	7.67	2.18	1.43	0.64	0.34	3.03	1.60
2	7.26	2.06	1.40	0.57	0.28	2.84	2.10
3	7.96	2.13	1.57	0.66	0.32	3.19	2.53
4	7.99	2.18	1.59	0.65	0.38	3.23	2.20
5	7.97	2.14	1.59	0.67	0.37	3.22	2.43
6	8.09	2.17	1.60	0.68	0.46	3.34	2.32
7	7.91	2.17	1.61	0.69	0.43	3.29	2.32
8	7.96	2.18	1.61	0.66	0.41	3.24	2.26
9	8.04	2.16	1.60	0.67	0.43	3.23	2.63

TABLE 22. Pooled within-locality variance-covariance matrix for males of *C. puritana* and *C. cuprascens*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "940"=0.0940.

					Character			
		1	2	3	4	5	6	7
Character	1	940	222	182	85	16	267	383
	2		79	51	25	5	83	74
	3			50	21	−1	64	70
	4				20	−5	29	21
	5					67	−0	−30
	6						128	117
	7							4332

Table 23. Pooled within-locality variance-covariance matrix for females of *C. puritana* and *C. cuprascens.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "751"=0.0751.

					Character			
		1	2	3	4	5	6	7
Character	1	751	137	108	71	39	254	−161
	2		48	27	16	8	53	−28
	3			37	14	8	45	−54
	4				16	2	28	−5
	5					56	7	9
	6						129	−128
	7							3595

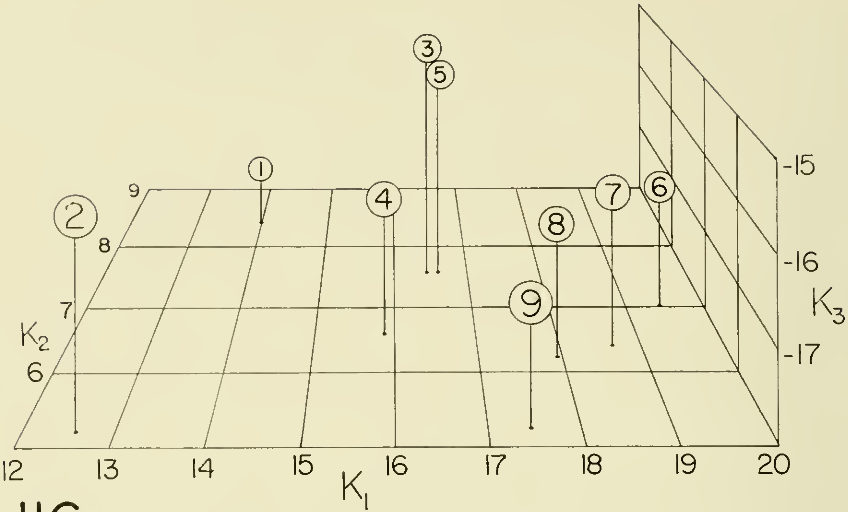
males and 55.300 for females. The first three components for males and the first two for females are highly significant ($p < 0.01$), and the fourth component for males is significant at the 5% level. The third component for females is on the borderline of being significant at the 5% level. The first three functions account for 83.47% of the variance (among localities relative to that within) in males and 93.13% in females. The distributions of the means in the first three discriminant functions are shown in Figures 116 and 117. Localities 1 and 2 are rather distantly separated from the others, which form a loose cluster in males and a tighter one in females.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 3 vs. 5 for both sexes, and 3 vs. 4, 4 vs. 5, 4 vs. 8, 4 vs. 9, 5 vs. 8, 5 vs. 9, 6 vs. 7, and 8 vs. 9 for females. Thus, the samples of *C. puritana* and *C. cuprascens* from Alabama are quite different from each other and from the other samples, which are more similar to each other.

Sets of vectors (Figs. 118 and 119), plotted for the first two functions, show the geographic trends of the seven characters when compared with Figures 116 and 117. Specimens from localities 1 and 2 are characterized by having relatively wider elytra and narrower heads. Specimens from western Kansas, Oklahoma, and Colorado (localities 6-9) have wider labra and middle bands and narrower elytra.

The results of the color analysis are shown in Figure 120. Populations northeast of eastern Kansas (including *C. puritana*) consist mostly of dark red-green, green, or blue-green individuals, with occasional blue individuals. Southwest of eastern Kansas, many individuals are reddish, often bright red.

On the basis of the statistical analysis, the specimens from Alabama seem distinct enough to separate as a subspecies; however, this is probably not wise at present because no samples were measured from areas between there and



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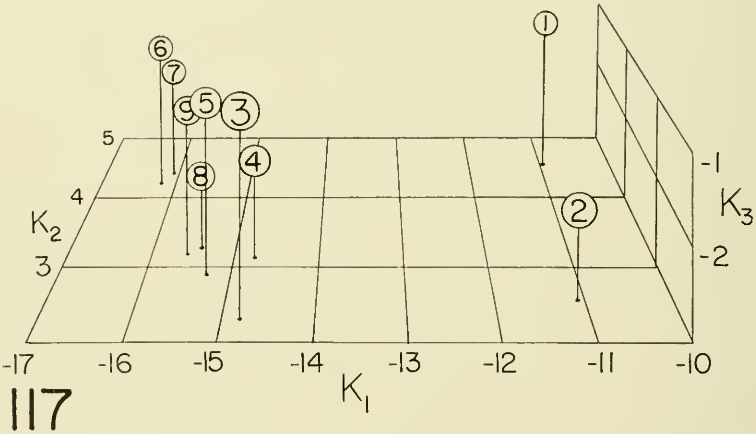

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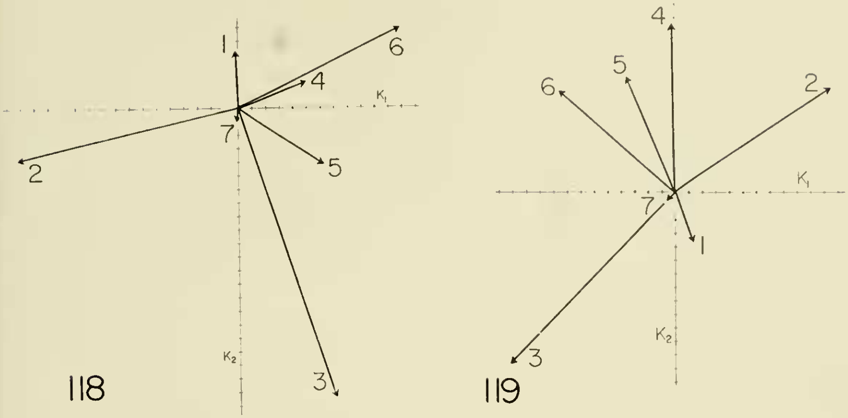
Figs. 116-117. Distributions of the means of the nine localities for males (Fig. 116) and females (Fig. 117) of *C. puritana* and *C. cuprascens* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.



FIGS. 118-119. Vectors for the seven characters of males (Fig. 118) and females (Fig. 119) of *C. puritana* and *C. cuprascens* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 116-117.

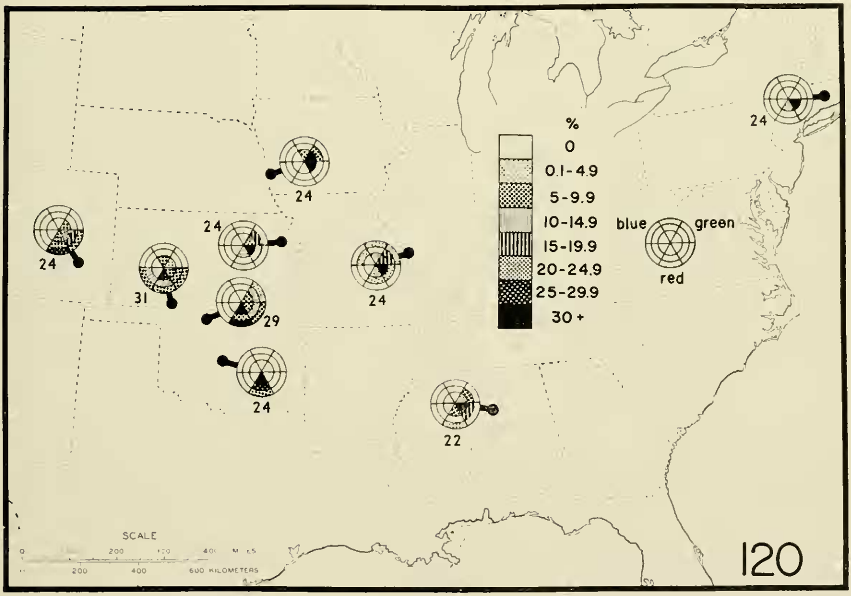


FIG. 120. Results of color analysis of *C. puritana* and *C. cuprascens* using the color wheel. Different degrees of shading indicate different percentages of the sample. The position of the three major colors are shown at right center. Numbers show the sample size for each locality.

Oklahoma or Missouri. The few specimens I have examined from these intervening areas, however, appear more like those from Missouri or Oklahoma than from Alabama. I have not seen specimens from Georgia. The color analysis suggests the populations in southern Kansas, Colorado, and Oklahoma, with many red individuals, might be worth naming, but the statistical analysis shows that the females are not distinct enough, although males are quite distinct. Thus, I recognize no subspecies within *C. cuprascens.* As the statistical analysis showed, *C. puritana* is quite different from *C. cuprascens*, even though only one of the characters in Table 18 was measured.

The closest relatives to *C. cuprascens* are *C. puritana* and *C. macra.* The former is restricted to the northern Atlantic Coastal Plain, while the latter is sympatric with *C. cuprascens* throughout most of their ranges. However, *C. macra* does not occur east of the Mississippi River in the South, as *C. cuprascens* does. This could indicate that *C. cuprascens* and *C. macra* evolved on opposite sides of the Mississippi valley, but not necessarily so. No other explanation is readily apparent. It does appear, at least, that *C. cuprascens* was once more widespread along the southeastern coastal plain than it now is, since the Alabama populations are so far separated from other known populations. As its coastal plain populations were exterminated by climatic changes during the Pleistocene, the more northeastern ones apparently became isolated and evolved into *C. puritana.* The spread of *C. cuprascens* northwestward into the range of *C. macra* has probably occurred rather recently (late Pleistocene), since populations in this area are rather similar. Its spread into the Pecos River system probably occurred via the Canadian River through northwestern Texas (the headwaters of the two river systems are very close in New Mexico).

As is the case in other species, the predominance of red color in populations from southern Kansas, Oklahoma, and Colorado is almost certainly due to their living on red soils (or having recently dispersed from areas of red soil). Red individuals also occur in New Mexico, Texas, Arkansas, Wyoming, and Montana.

C. fulgida

This is primarily a northern species, which is most common in the Great Plains north of Texas (Fig. 121). Its distribution by counties or states is as follows:

MANITOBA; SASKATCHEWAN; ALBERTA; MONTANA: Gallatin, Prairie, Roosevelt, Sheridan; NORTH DAKOTA: Benson, Bottineau, Burke, Burleigh, Dickey, Divide, Dunn, Grand Forks, McLean, McHenry, Mercer, Montrail, Oliver, Pierce, Roulette, Slope, Stutsman; MINNESOTA; SOUTH DAKOTA: Beadle, Brookings, Edmund, Fall River, Kingsbury; WYOMING: Albany, Carbon, Goshen, Weston; COLORADO: Arapahoe, Bent, Conejos, Crowley, El Paso, Fremont, Huerfano, Larimer, Logan, Otero, Prowers, Sedgwick, Summit,

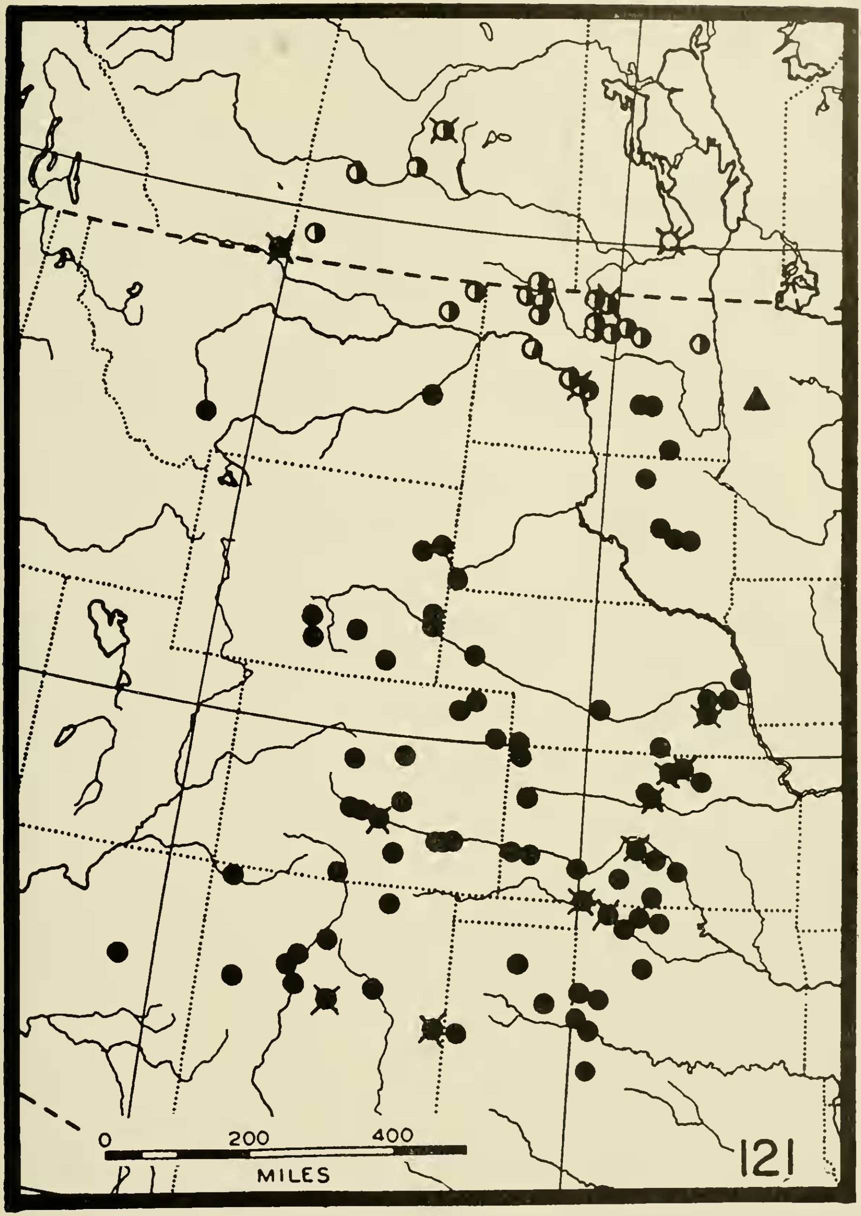


Fig. 121. Known distribution of *C. fulgida*. Open circle=*C. f. westbournei*, shaded circle=*C. f. fulgida*, half-shaded circle=intergrade population, triangle=state record, circles with "X" are localities included in the statistical analysis.

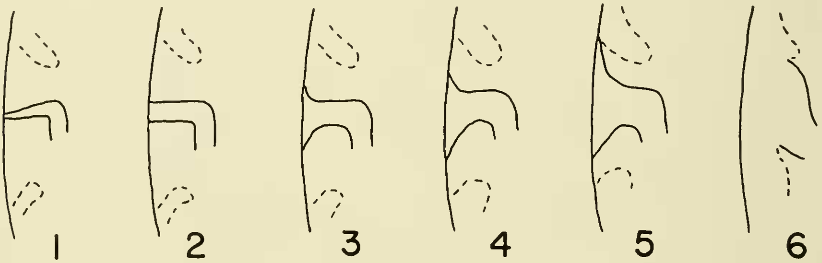
Weld, Yuma; NEBRASKA: Dawson, Douglas, Dundy, Lancaster, Morrill, Nuckolls, Saunders; KANSAS: Barber, Cheyenne, Clark, Clay, Cloud, Ford, Hamilton, Kearney, Kiowa, Lincoln, Reno, Republic, Sedgwick, Stafford, Wallace; OKLAHOMA: Alfalfa, Beckham, Blaine, Harmon, Jackson, Woods; TEXAS: Bailey, Donley, Hemphill, Hutchinson, Knox; NEW MEXICO; Bernalillo, Colfax, Guadalupe, Sandoval, San Juan, Torrance, Valencia; ARIZONA: Navajo. *Doubtful localities:* "Fla." and Woodward (La Salle Co.?), Texas.

The following forms have been described within this species:

Cicindela fulgida Say, 1823. Type locality: Missouri Territory, near the mountains on the Platte and Arkansas Rivers.
Cicindela fulgida elegans Calder, 1922. Type locality: Westbourne, Manitoba, Canada. *Preoccupied.*
Cicindela fulgida subnitens Calder, 1922. Type locality: Lincoln, Nebraska.
Cicindela fulgida westbournei Calder, 1922. New name for *C. f. elegans.*
Cicindela fulgida pseudowillistoni W. Horn, 1938. Type locality: Lake Como, southern Wyoming.

In recent years, two subspecies have been recognized: *C. f. westbournei*, the small, dark colored northern form, and *C. f. fulgida*, the bright, usually red southern form.

In studying geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 122); (6) smallest width of transverse portion of middle band (Fig. 123). Specimens from 14 localities were measured; the localities and sample sizes are given in Table 24. Sample sizes were adequate except for two localities each in Canada and New Mexico. Specimens from two localities in Saskatchewan and two in Colorado were lumped into one sample each.



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FIGS. 122-123. Illustrations of certain characters measured on elytra of *C. fulgida*; FIG. 122, arbitrary units for shapes of base of middle band; FIG. 123, smallest width of transverse portion of middle band.

Table 24. Localities and sample sizes of the specimens of *C. fulgida* measured.

Locality	N ♂	N ♀
1. MANITOBA, Westbourne	12	12
2. SASKATCHEWAN, Route 14, s.e. of Blucher; between Clavet and Elston	6	2
3. ALBERTA, Onefour	5	6
4. NORTH DAKOTA, Bottineau Co., near Bottineau	12	12
5. NORTH DAKOTA, Oliver Co., Sect. 35, Twp. 144, Rg. 83	12	12
6. COLORADO, Fremont Co., 3 mi. s. of Penrose, near Portland	9	12
7. NEBRASKA, Lancaster Co., Lincoln (west edge)	12	11
8. KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	10	12
9. KANSAS, Republic Co., 4 mi. w., 1 s. of Kackley	12	12
10. KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	12	12
11. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
12. KANSAS, Clark Co., Englewood	12	12
13. OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	11	8
14. NEW MEXICO, Roosevelt Co., 4 mi. e., 1 s. of Arch	4	3
15. NEW MEXICO, Torrance Co., 4 mi. s.e. of Willard	2	8

The means for the characters and localities are given in Tables 25 and 26. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 27 and 28. The sums of the among-locality variance components are 83.504 for males and 69.975 for females. The first two components for males and the first three for females are highly significant ($p < 0.01$), and the third component for males is significant at the 5% level. The first three functions account for 96.50% of the variance (among localities relative to that within) in males and 94.63% in females. The distributions of the means in the first three discriminant functions are shown in Figures 124 and 125. Localities in the central United States and eastern New Mexico form a tight cluster, while the other localities are rather widely separated from one another and from the cluster.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 7 vs. 10, 9 vs. 11, 9 vs. 13, 11 vs. 12, 11 vs. 13, 12 vs. 13, 8 vs. 14, and 11 vs. 14 for both sexes; 8 vs. 10, 9 vs. 10, 9 vs. 12, 10 vs. 11, 10 vs. 12, 10 vs. 13, 9 vs. 14, and 10 vs. 14 for males; and 7 vs. 13, 8 vs. 9, 12 vs. 14, and 13 vs. 14 for females. Thus, the members of the cluster are generally not significantly different from one another, while the isolated samples are different from one another and the cluster.

Sets of vectors (Figs. 126 and 127), plotted for the first two functions, show geographic trends in the six characters when compared with Figures

TABLE 25. Means of 15 localities (see Table 24) and six characters for males of *C. fulgida*. Values for characters 1-4 and 6 are in mm.

	Character					
Locality	1	2	3	4	5	6
1	6.56	2.01	1.62	0.78	4.46	0.90
2	6.64	2.07	1.62	0.74	4.05	1.05
3	7.38	2.19	1.81	0.87	4.88	1.06
4	6.91	2.09	1.72	0.83	3.87	0.85
5	6.66	2.02	1.63	0.76	3.34	0.78
6	7.30	2.20	1.81	0.90	4.11	0.92
7	6.83	2.06	1.63	0.77	2.60	0.70
8	7.05	2.11	1.69	0.81	2.62	0.83
9	7.04	2.07	1.68	0.80	2.37	0.71
10	6.92	2.07	1.67	0.78	2.39	0.73
11	6.98	2.08	1.70	0.80	2.37	0.72
12	6.92	2.07	1.68	0.77	2.12	0.63
13	7.01	2.11	1.69	0.80	2.10	0.67
14	7.26	2.16	1.77	0.83	2.75	0.83
15	6.73	2.10	1.65	0.80	5.60	1.34

TABLE 26. Means of 15 localities (see Table 24) and six characters for females of *C. fulgida*. Values for characters 1-4 and 6 are in mm.

	Character					
Locality	1	2	3	4	5	6
1	6.94	2.21	1.72	0.86	3.84	0.81
2	7.04	2.25	1.73	0.84	3.40	0.88
3	7.40	2.39	1.87	0.94	4.28	1.02
4	7.22	2.32	1.84	0.93	3.48	0.82
5	6.95	2.17	1.73	0.85	2.97	0.74
6	7.69	2.42	1.95	1.00	3.26	0.93
7	7.04	2.19	1.71	0.83	2.27	0.61
8	7.20	2.18	1.76	0.87	2.20	0.76
9	7.26	2.21	1.76	0.88	2.13	0.71
10	6.98	2.13	1.70	0.81	2.18	0.67
11	7.26	2.24	1.79	0.86	2.17	0.70
12	7.26	2.25	1.78	0.84	2.02	0.66
13	7.25	2.26	1.76	0.87	2.08	0.64
14	7.39	2.29	1.84	0.89	2.10	0.81
15	7.00	2.18	1.73	0.86	5.03	1.30

124 and 125. Specimens with high values in K_1 have longer labra, wider markings, and relatively shorter elytra. Specimens with high values in K_2 have wide labra, narrow elytra (in males; wide in females), and narrower middle bands.

The results of this analysis show that, except for locality 15, there are no

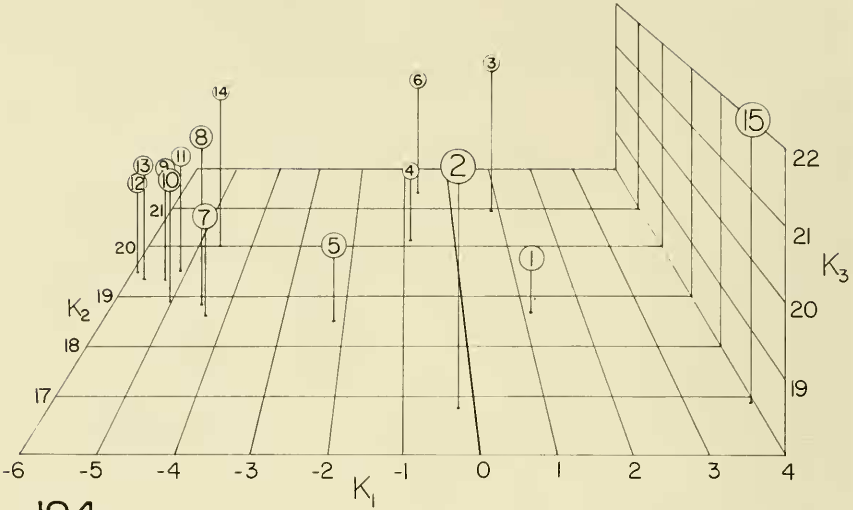
Table 27. Pooled within-locality variance-covariance matrix for males of *C. fulgida*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "690"=0.0690.

Character	1	2	3	4	5	6
1	690	140	137	90	274	129
2		49	36	23	67	29
3			42	24	64	30
4				23	33	18
5					1549	228
6						119

Table 28. Pooled within-locality variance-covariance matrix for females of *C. fulgida*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "691"=0.0691.

Character	1	2	3	4	5	6
1	691	160	141	103	114	77
2		62	38	27	16	19
3			42	27	23	15
4				26	5	11
5					2326	231
6						153

clear groupings that could be called subspecies. The tight cluster that is separated from other samples is probably an artifact caused by the nonrandom geographical distribution of the samples; if samples had been included from South Dakota, Wyoming, and Montana, they would probably fill in the gap. There appears to be a gradual cline running from larger, narrowly marked populations in the south to smaller, widely marked northern populations. Thus, on the basis of this analysis alone, the subspecies *C. f. westbournei*, representing one end of a cline, cannot be recognized. However, a character that was not measured sets it apart from all other populations: the shape of the apex of the aedeagus. In specimens from Westbourne, Manitoba, the apex of the aedeagus is rather evenly tapered and comparatively blunt; in specimens from all other localities, it is more prolonged and slender (Figs. 128-136). Another characteristic of specimens from Westbourne is their dark dorsal color, ranging from dark purplish red to black, often with a bluish sheen. Only three out of 39 specimens before me, or about 7.5%, have brighter colors (two are reddish, one is yellow-green). Specimens from other Canadian localities, northeastern Montana, and northern North Dakota exhibit a great variety of colors, ranging from dark purple to red to red-green to green to blue-green to blue to purple-blue. Green-red specimens are also



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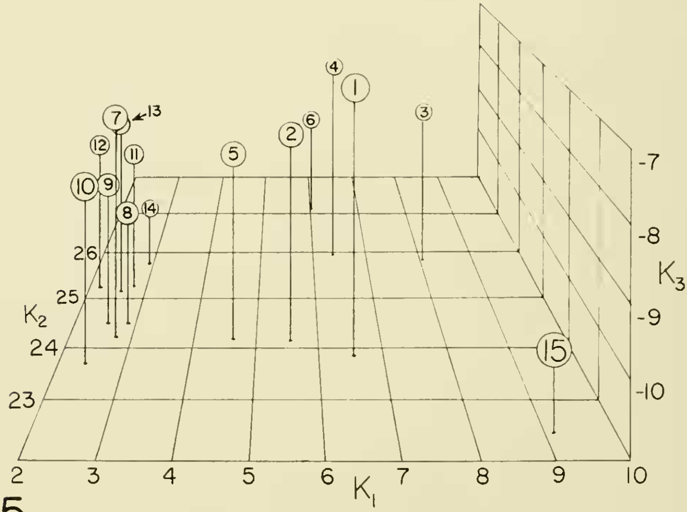

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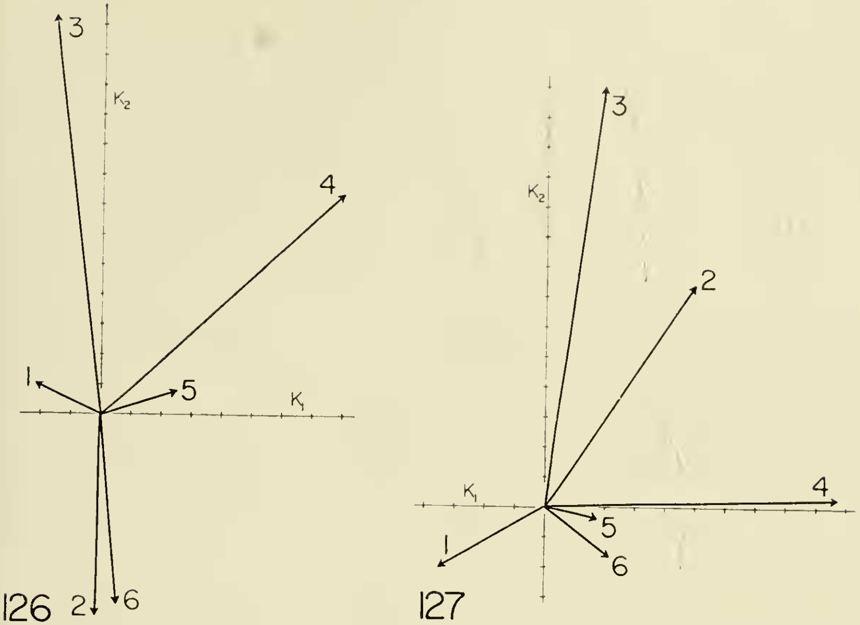
FIGS. 124-125. Distributions of the means of the 15 localities for males (Fig. 124) and females (Fig. 125) of *C. fulgida* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.

known from southwestern Montana, southern Wyoming, and central Colorado. The population at Grants, New Mexico, is said to contain many blue individuals (Rumpp, *in litt.*). The population at Lincoln, Nebraska, contains about 40% dark purple or black individuals. Specimens examined from other

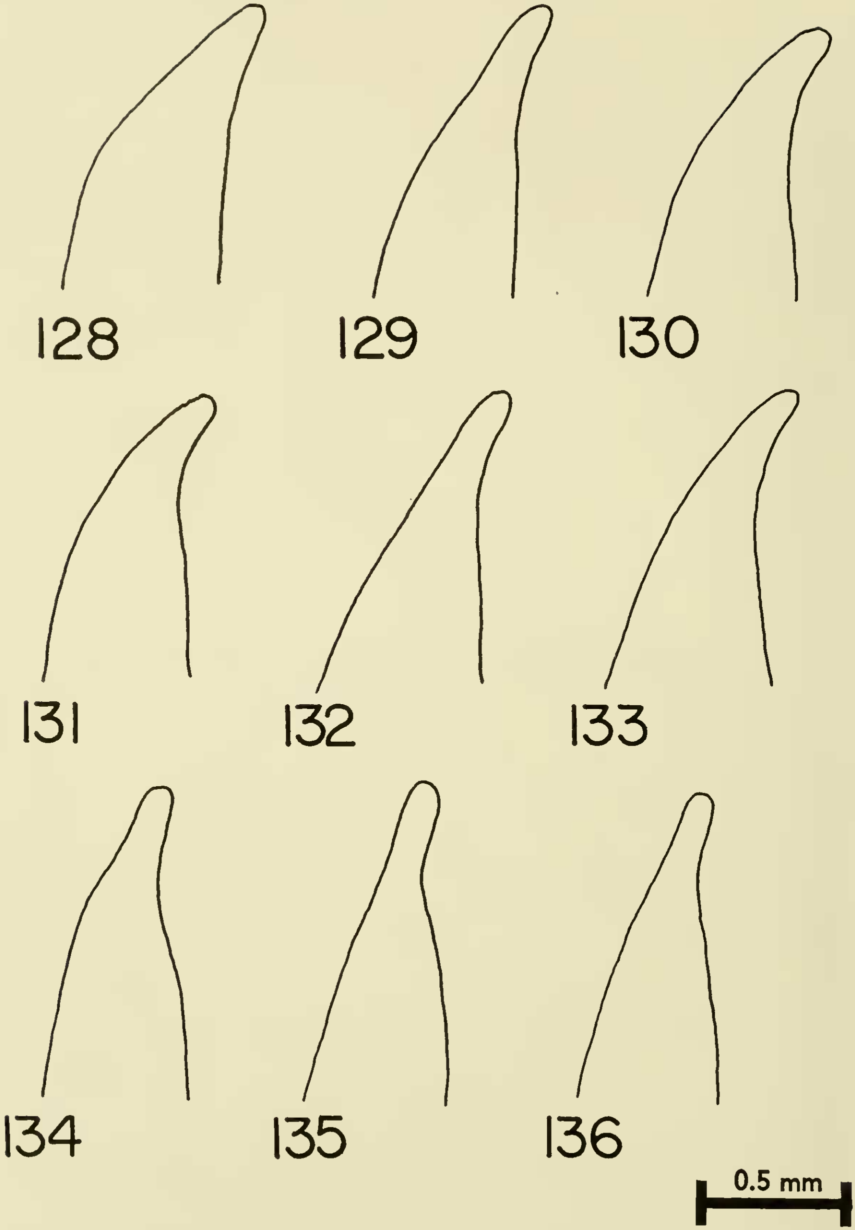


Figs. 126-127. Vectors for the six characters of males (Fig. 126) and females (Fig. 127) of *C. fulgida* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 124-125.

localities are bright red to red-purple, with occasional red individuals having a green sheen. It is not known whether northern or western populations exhibit a seasonal change of color as was noted for those from the central United States (see section on post-emergence changes of the adult).

Because of its genitalic difference, nearly uniform dark color, and its isolated geographic location, *C. f. westbournei* will be retained as a poorly differentiated subspecies, at least for the present. The populations of small individuals with quite variable color in Saskatchewan, northeastern Montana, and northern North Dakota could be considered as intermediates (Fig. 121).

Specimens with the markings wide and connected (particularly the apex of the humeral lunule and transverse portion of the middle band) are found in scattered localities in the northern and western parts of the range of the species: all Canadian localities, eastern Montana, northern North Dakota, Wyoming, south-central Colorado, and central New Mexico. Especially widely maculate individuals are found in populations from Carbon County, Wyoming, and Torrance County, New Mexico (locality 15 in the statistical analysis). This form was named *pseudowillistoni* by W. Horn, but because of its scattered and nonuniform distribution (it could be called polytopic), it is best not recognized as a subspecies.



Figs. 128-136. Apex of aedeagus (dorsal aspect) of *C. fulgida* from various localities: Westbourne, Manitoba (Fig. 128); near Blucher, Saskatchewan (Fig. 129); Onefour, Alberta (Fig. 130); near Bottineau, North Dakota (Fig. 131); Oliver County, North Dakota (Fig. 132); Rawlins, Wyoming (Fig. 133); 4 miles northwest of Jamestown, Kansas (Fig. 134); 2.5 miles southwest of Plainview, Oklahoma (Fig. 135); 4 miles southeast of Willard, New Mexico (Fig. 136).

The closest relative of *C. fulgida* is *C. parowana*, which is found in the Great Basin, western Oregon, western Washington, and southern British Columbia. Except for a longer labrum and several differences of the male genitalia, it is quite similar to *C. fulgida* in general appearance and range of variation of color and maculation. Quite clearly, they evolved from a common ancestor that was probably widespread in the western United States and Canada in late Tertiary times. The rising mountains of the Cascadian Revolution apparently separated it into populations which became differentiated into the two modern species. *C. fulgida* is basically a species of cool climates; however, Pleistocene glaciers and the accompanying shift of climatic zones no doubt drove it south. As climates warmed and it moved northward again, relict populations were left in Arizona, New Mexico, and Texas (the locality of Woodward, Texas, listed as a doubtful locality earlier, may actually be a relict population in south-central Texas). The occurrence of dark individuals at Lincoln, Nebraska, a characteristic of more northern populations, may be explained by assuming that the species was not exterminated from there by the later glaciations and became dark due to the cool climate of that time.

C. macra

This species occurs between the Rocky and Appalachian Mountains (Fig. 137). Its distribution by counties or states is as follows:

MICHIGAN: Berrien, Emmet, Leelanau; WISCONSIN: Dane, St. Croix, Waushara, Wood; MINNESOTA: Ramsey, Scott, Wabasha, Washington; OHIO; INDIANA: Greene, Lake, Monroe, Porter, Posey, Putnam, Vigo; KENTUCKY: Henderson; TENNESSEE; ILLINOIS: Calhoun, Carroll, Cook, Mason, Morgan, Ogle, Whiteside; IOWA: Alexander, Benton, Blackhawk, Boone, Clinton, Des Moines, Johnson, Lee, Linn, Louisa, Monona, Pottawatamie, Van Buren, Woodbury; MISSOURI: Atchison, Clay or Jackson, Holt; ARKANSAS: Craighead, Crawford; LOUISIANA; TEXAS: Childress, Dallas, Denton, Eastland, Grayson, Hall, Hardeman, Hemphill, Kaufman, Montague, Potter, Randall, Stonewall, Wichita, Wilbarger; OKLAHOMA: Alfalfa, Beaver, Beckham, Caddo, Choctaw, Cimarron, Cleveland, Comanche, Cotton, Custer, Dewey, Ellis, Greer, Harmon, Harper, Hughes, Jackson, Johnston, Kingfisher, Kiowa, Logan, Love, Major, Marshall, McClain, Osage-Payne Co. line, Payne, Pontotoc, Roger Mills, Seminole, Texas, Woods, Woodward; KANSAS: Barber, Barton, Cheyenne, Clark, Clay, Comanche, Cowley, Douglas, Ellsworth, Kearney, Kiowa, Leavenworth, McPherson, Meade, Mitchell, Ness, Osbourne, Phillips, Pottawatomie, Reno, Riley, Rooks, Russell, Sedgwick, Shawnee, Stafford, Sumner, Trego; COLORADO: Denver, Larimer; WYOMING: Carbon; NEBRASKA: Brown, Buffalo, Cass, Chase, Cherry, Dakota, Dixon, Douglas, Dundy, Franklin, Hamilton, Lancaster, Madison, Merrick, Otoe, Platte, Saunders, Thomas; SOUTH DAKOTA: Brookings, Clay, Union. Towns that could not be located: Pine, Indiana; Adams and Herrold, Iowa. *Doubtful records:* Shoshone, Inyo County, California; Las Cruces, Dona Ana County; Socorro, Socorro County; and Albuquerque, Bernalillo County, New Mexico.

This species could be considered a sibling to *C. cuprascens* and *C. puritana* (see Table 18 for a comparison of the three), and they have been confused in the past, leading to erroneous records in the literature and misidentified specimens in museum collections. The ranges of *C. macra* and *C. cuprascens* overlap broadly, but there are notable areas of nonoverlaping; for example, *C. macra* is rare northwest of South Dakota and Wyoming, but *C. cuprascens*

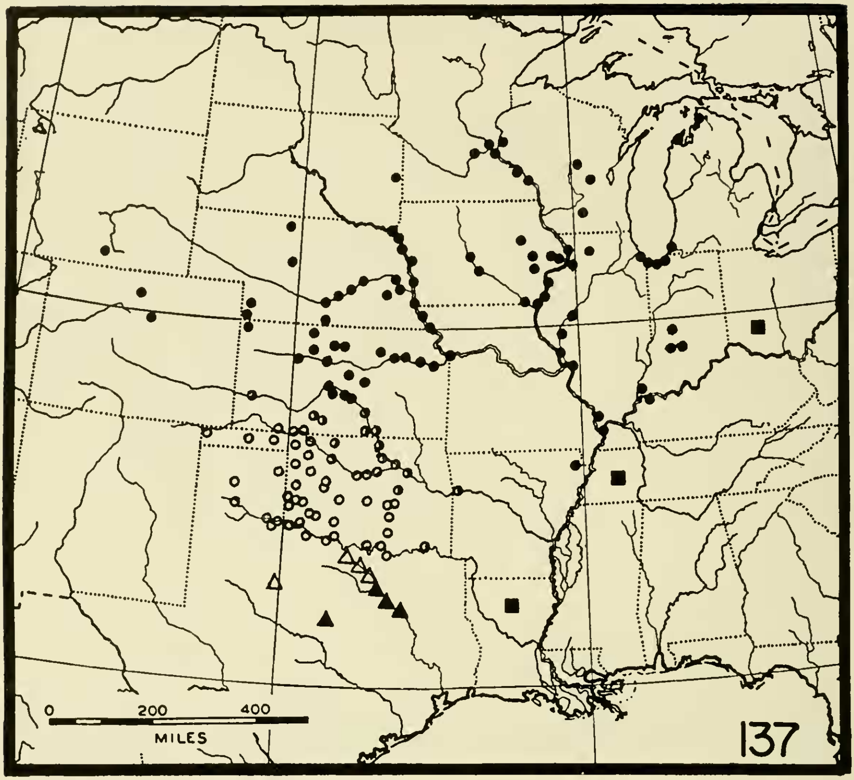


FIG. 137. Known distribution of *C. macra*. Shaded circle=*C. m. macra*, open circle=*C. m. fluviatilis*, half-shaded circle=intergrade population between *C. m. macra* and *C. m. fluviatilis*, shaded triangle=*C. m. amplicata*, open triangle=intergrade population between *C. m. fluviatilis* and *C. m. amplicata*, square=state record.

occurs as far north as Manitoba and Montana; *C. cuprascens* is absent from Michigan, where *C. macra* occurs; finally, *C. macra* does not occur in Alabama or Georgia, where *C. cuprascens* has been found. These two species also occupy the same ecological microhabitat; I have often seen them running together on the same sandbar. Nevertheless, out of dozens of mating pairs that I have collected, none involved two individuals of the wrong species. Also, no specimens that appear to be hybrids have been seen. Thus, I have no doubt that these forms are specifically distinct and genetically separate.

The following forms have been described within this species:

Cicindela macra Leconte, 1860. Type locality: Wisconsin and Minnesota (types bear yellow paper circles, signifying "Illinois, Missouri, and Central Valley").
Cicindela macra mercurialis Casey, 1913. Type locality: Iowa.
Cicindela macra topeka Casey, 1916. Type locality: Mt. Hope, Kansas.

Cicindela macra fluviatilis Vaurie, 1951. Type locality: Red River, north of Quanah, Hardeman County, Texas.
Cicindela macra amplicata Vaurie, 1951. Type locality: Denton County, Texas.

In recent years, three subspecies have been recognized: *C. m. macra*, the smallest dark green or green-brown form found north and east of Oklahoma; *C. m. fluviatilis*, the large, reddish, widely maculate form in Oklahoma and northwestern Texas; and *C. m. amplicata*, the large, dark green, narrowly maculate form in north-central Texas.

The following characters were measured in the study of geographic variation: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) width of middle band at a specified place (Fig. 114); (6) width of head; (7) shape of apex of middle band in arbitrary units (Fig. 115); (8) color of elytra, using color wheel.

Table 29. Localities and sample sizes of the specimens of *C. macra* measured.

Locality	N ♂	N ♀
1. INDIANA, Monroe Co., Bloomington	5	9
2. MINNESOTA, Wabasha Co., Dumfries; Scott Co., Jordan; Washington Co., Gray Cloud Island; WISCONSIN, St. Croix Co., North Hudson	12	10
3. IOWA, Woodbury Co., Sergeant Bluff	12	11
4. KANSAS, Ellsworth Co., Kanopolis Lake, s.e. Ellsworth Co.	12	11
5. KANSAS, Sumner Co., just n. of Geuda Springs	12	12
6. OKLAHOMA, Alfalfa Co., 3 mi. n., 5 e. of Cherokee	12	12
7. OKLAHOMA, Cleveland Co.	12	12
8. OKLAHOMA, Marshall Co., Lake Texoma State Park	12	9
9. TEXAS, Montague Co., Forestburg	12	8

Specimens from nine localities were measured; the localities and sample sizes are given in Table 29. Sample sizes were adequate from nearly all localities; however, specimens from Minnesota and Wisconsin were lumped into one sample.

The means for the characters and localities are given in Tables 30 and 31. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters for both sexes (except characters 1 and 7 for males, which are significant at the 5% level). Pooled within-locality variance-covariance matrices are given in Tables 32 and 33. The sums of the among-locality variance components are 54.793 for males and 62.362 for females. The first two components for males and the first three for females are highly significant ($p < 0.01$), and the fourth for females is significant at the 5% level. The first three functions account for 95.31% of the variance (among localities relative to that within)

Table 30. Means of nine localities (see Table 29) and seven characters for males of *C. macra*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	8.09	2.04	1.60	0.71	0.45	3.04	4.60
2	7.89	2.01	1.56	0.67	0.33	3.03	3.52
3	8.08	2.02	1.61	0.69	0.39	3.09	3.72
4	8.09	2.09	1.63	0.70	0.39	3.14	4.08
5	8.27	2.12	1.67	0.74	0.47	3.20	3.86
6	8.18	2.11	1.69	0.74	0.55	3.26	3.92
7	8.17	2.11	1.69	0.72	0.71	3.29	3.92
8	8.12	2.09	1.69	0.73	0.70	3.23	3.64
9	8.42	2.27	1.75	0.78	0.42	3.37	3.41

Table 31. Means of nine localities (see Table 29) and seven characters for females of *C. macra*. Values for characters 1-6 are in mm.

				Character			
Locality	1	2	3	4	5	6	7
1	8.20	2.04	1.64	0.66	0.37	3.17	3.76
2	7.79	1.95	1.54	0.60	0.30	3.03	3.21
3	8.33	2.05	1.64	0.67	0.35	3.24	3.93
4	8.36	2.11	1.68	0.70	0.46	3.35	3.75
5	8.54	2.15	1.75	0.73	0.41	3.42	3.51
6	8.78	2.31	1.78	0.77	0.60	3.53	3.60
7	8.66	2.25	1.77	0.73	0.59	3.54	4.18
8	8.77	2.30	1.81	0.74	0.58	3.54	4.10
9	9.04	2.43	1.83	0.77	0.41	3.65	3.44

Table 32. Pooled within-locality variance-covariance matrix for males of *C. macra*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1104"=0.1104.

					Character			
		1	2	3	4	5	6	7
Character	1	1104	230	171	75	40	280	412
	2		71	40	21	3	66	117
	3			46	20	2	61	59
	4				24	2	33	39
	5					124	6	79
	6						120	144
	7							4337

TABLE 33. Pooled within-locality variance covariance matrix for females of *C. macra.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^4; thus "1076"=0.1076.

					Character			
		1	2	3	4	5	6	7
Character	1	1076	226	187	104	72	365	217
	2		81	43	29	16	82	47
	3			55	23	16	76	36
	4				26	0	43	66
	5					102	11	64
	6						174	70
	7							4406

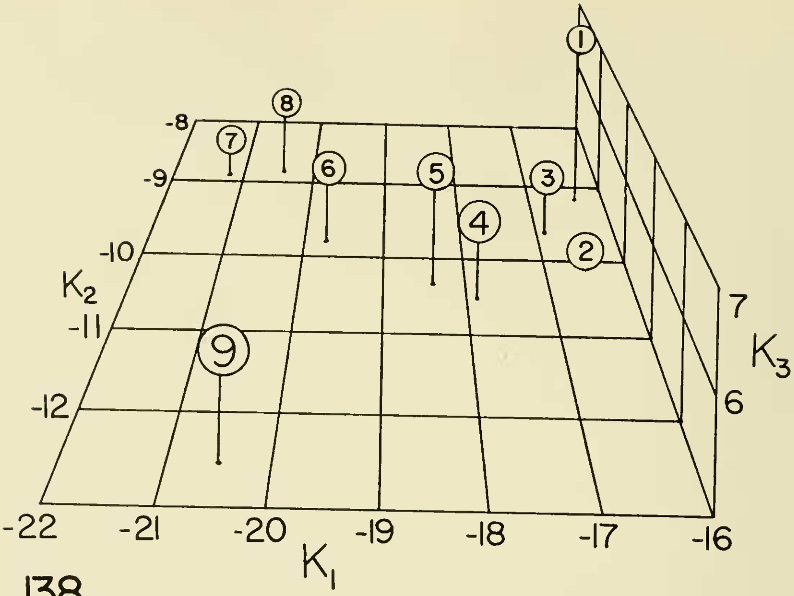
in males and 92.86% in females. The distributions of the means in the first three discriminant functions are shown in Figures 138 and 139 (however, the third function is not significant in males and could be ignored). Locality 9 is widely separated from the others, which form an elongate, loose cluster in males and three more compact clusters in females.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 1 vs. 3, 4 vs. 5, and 7 vs. 8 in both sexes; 2 vs. 3 in males; and 1 vs. 2, 6 vs. 7. and 6 vs. 8 in females.

Sets of vectors (Figs. 140 and 141), plotted in the first two functions, show geographic trends of the seven characters when compared with Figures 138 and 139. Specimens from locality 9 have relatively wider and shorter elytra. Specimens from the northeastern localities have relatively long, narrow elytra and long labra. Specimens from Oklahoma have wide heads and broad middle bands.

The results of the color analysis are shown in Fig. 142. Populations from north and east of Oklahoma consist mostly of dark green to dark red-green to dark reddish (actually brown) individuals. Populations from Oklahoma consist of mostly brighter red individuals, with fewer red-green and green individuals. The Texas population is similar to the northeastern populations in color.

These analyses confirm the existence of the three recognized subspecies. Locality 9, representing *C. m. amplicata*, is greatly different from all others. Localities 1-5 *(C. m. macra)* are significantly different from localities 6-8 *(C. m. fluviatilis).* The inclusion of samples from other areas would no doubt fill in the gaps between the clusters in Figures 138 and 139. However, study of specimens from most of the localities in Figure 137 indicates that the variation within this species is in the form of a stepped cline, with narrow zones of intergradation between the three subspecies. In fact, three of the



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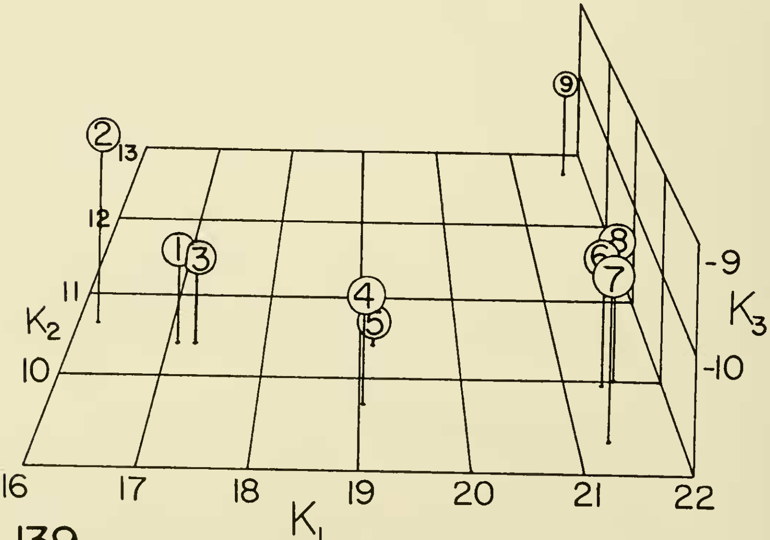

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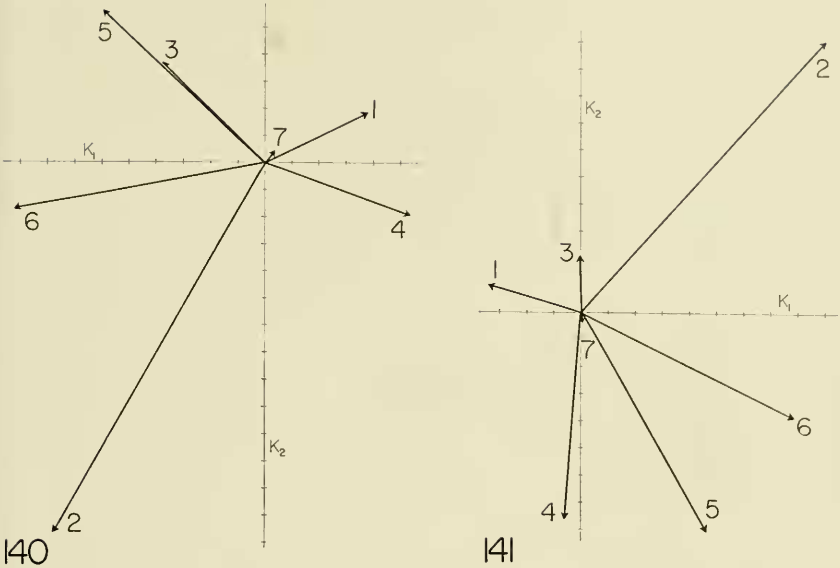
Figs. 138-139. Distributions of the means of the nine localities for males (Fig 138) and females (Fig. 139) of *C. macra* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.



Figs. 140-141. Vectors for the seven characters of males (Fig. 140) and females (Fig. 141) of *C. macra* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 138-139.

localities analyzed (5, 6, and 9) are in intergradation zones. Intergrade populations are characterized by much variability in color and maculation.

The fact that *C. macra* shows a greater differentiation into geographical races than does *C. cuprascens* might indicate that it has been in its present range (at least in the southern parts) for a longer time than *C. cuprascens.* If true, this also supports the idea that the two evolved on opposite sides of the Mississippi valley, as mentioned under *C. cuprascens.* The pattern of color variation of *C. macra* shows very clearly the effect of selection to match the substrate color. The limits of the reddish *C. m. fluviatilis* coincide almost exactly with the northeastern limits of red soil (Figs. 137 and 108). Populations intermediate between it and *C. m. macra* in southern Kansas, northeastern Oklahoma, and western Arkansas contain some reddish, some brown, and some green individuals. The area of occurrence of "true" *C. m. amplicata* possesses dark soil; however, in the northern and western parts of the range of this form, tan or reddish soils begin to appear, and populations contain many reddish and brown individuals.

This species is reported in the literature from three localities along the Rio Grande in New Mexico. No specimens have been seen from these localities, and they have been listed as doubtful. It is hard to imagine how the species could have gotten there.

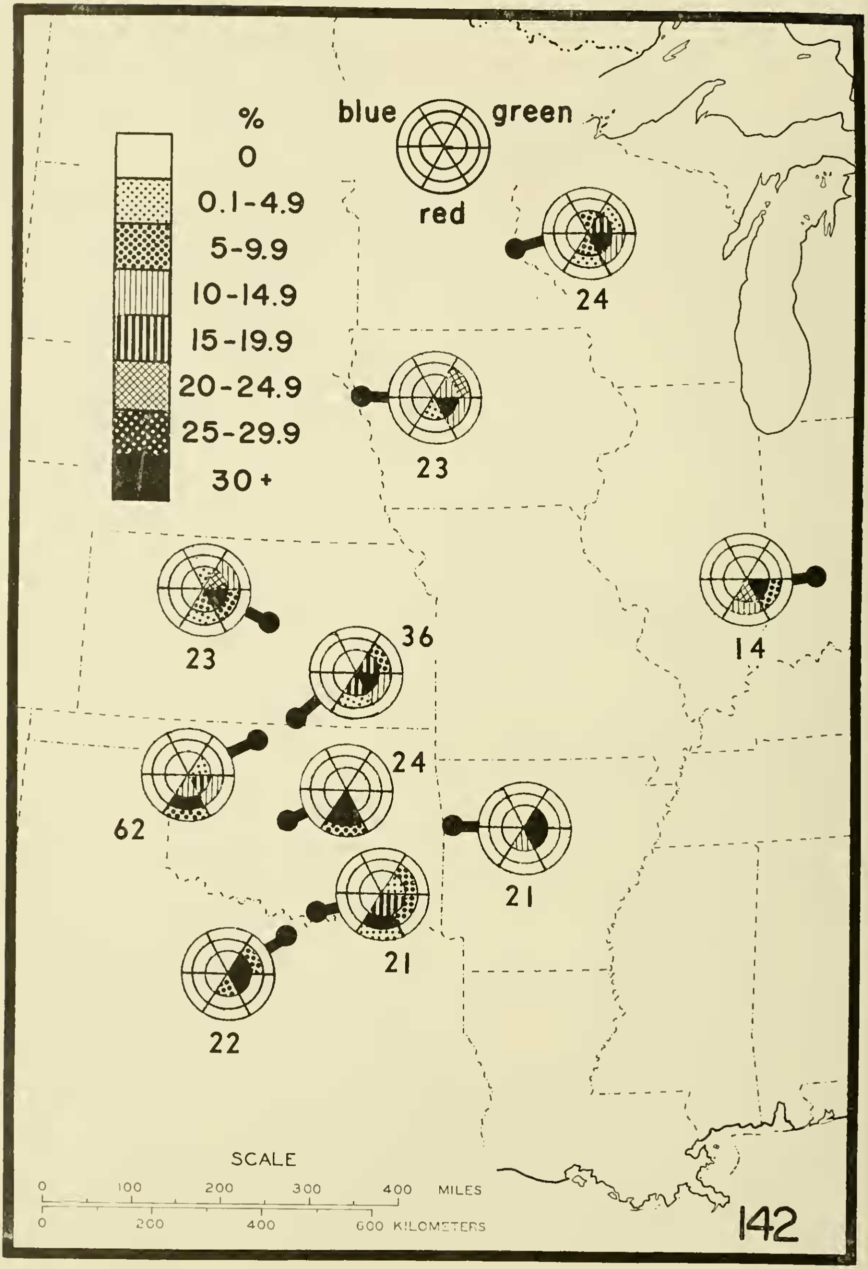


FIG. 142. Results of color analysis of *C. macra* using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three major colors are shown at top center. Numbers show the sample size for each locality.

C. nevadica

This is a western species, occurring from the Mojave Desert in California and Sonora, Mexico, to the western edge of the Central Plains (Fig. 143). Its distribution by counties or states is as follows:

ALBERTA; SASKATCHEWAN; MANITOBA; MONTANA: Hill, Prairie, Roosevelt, Sheridan, Yellowstone; NORTH DAKOTA: Pierce, Ramsey; SOUTH DAKOTA: Hand;

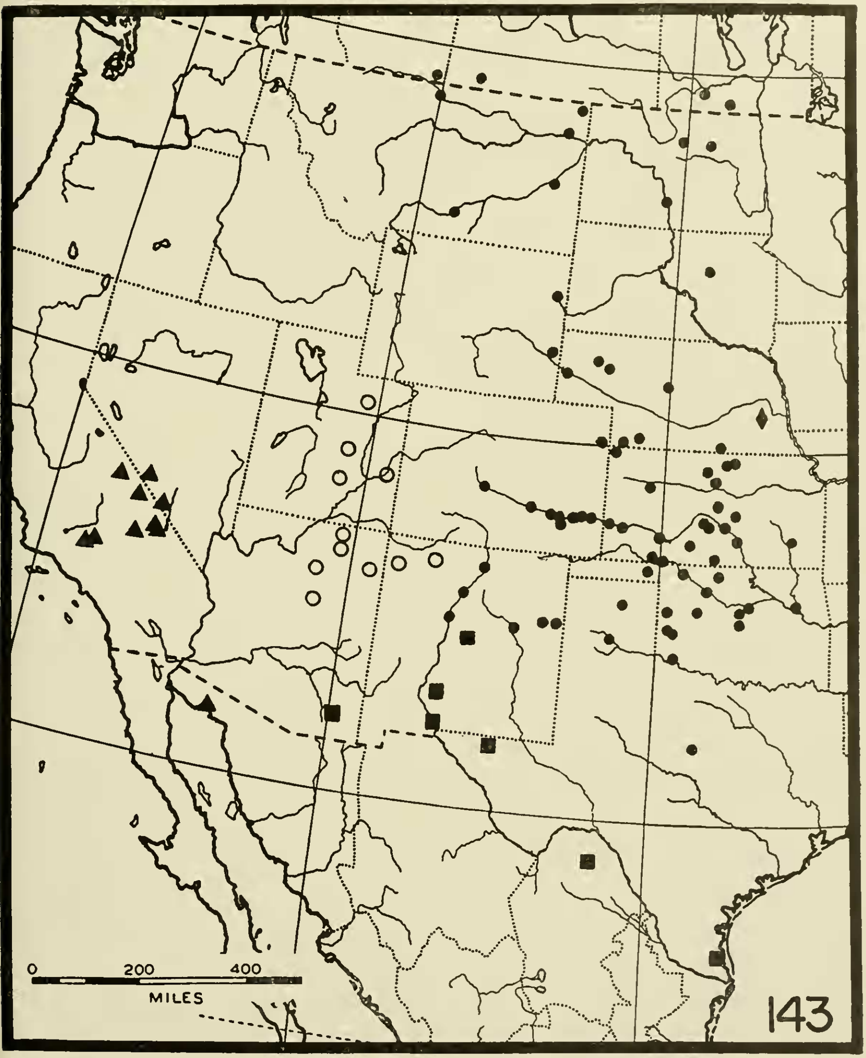


Fig. 143. Known distribution of *C. nevadica.* Triangle=*C. n. nevadica*, open circle=*C. n. tubensis*, shaded circle=*C. n. knausi*, square=*C. n. olmosa*, diamond=*C. n. lincolniana.*

WYOMING: Goshen, Weston; NEBRASKA: Dundy, Hitchcock, Lancaster, Nuckolls, Scotts Bluff, Sheridan; COLORADO: Bent, Chaffee, Prowers, Otero; KANSAS: Barber, Cheyenne, Clark, Cloud, Ellsworth, Ford, Gove, Hamilton, Kearney, Kiowa, Lincoln, McPherson, Meade, Mitchell, Reno, Republic, Russell, Sedgwick, Stafford, Sumner; OKLAHOMA: Alfalfa, Beaver, Beckham, Custer, Jackson, Logan, Major, Oklahoma, Payne, Roger Hills, Tulsa, Woods; TEXAS: Eastland, Hudspeth, Hutchinson, Kenedy, Randall; NEW MEXICO: Bernalillo, Dona Ana, Guadalupe, Quay, Rio Arriba, San Doval, San Juan, Santa Fe, Sierra, Taos, Torrance; UTAH: Duchesne, Emery, Moab, Wayne; ARIZONA: Apache, Cochise, Coconino, Navajo; NEVADA: Nye; CALIFORNIA: Inyo, Kern, San Bernadino; SONORA; COAHUILA. The exact location of Acnegas, Coahuila, Mexico, could not be found.

The following forms have been described within this species:

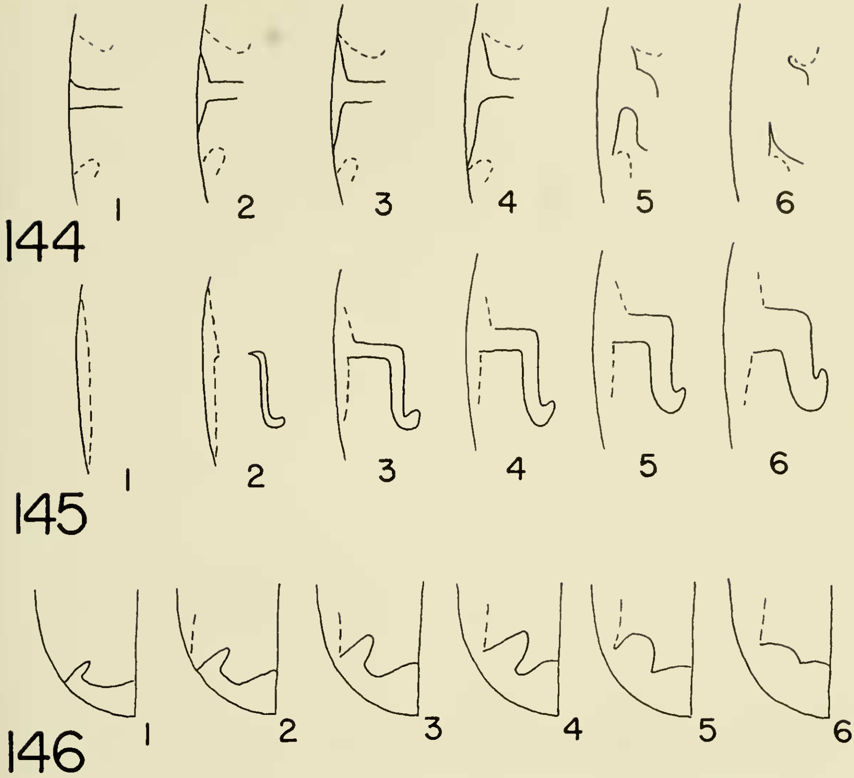
Cicindela nevadica Leconte, 1875c. Type locality: Nevada.
Cicindela Knausii Leng, 1902. Type locality: Kackley, Belvidere, and Great Spirit Springs, Kansas.
Cicindela lincolniana Casey, 1916. Type locality: Lincoln, Nebraska.
Cicindela nevadica tubensis Cazier, 1939. Type locality: Tuba City, Coconino County, Arizona.
Cicindela nenadica olmosa Vaurie, 1951. Type locality: Los Olmos, Kenedy County, Texas.

In recent years, all five of the above forms have been recognized as subspecies, *C. n. nevadica* being characterized by dark brown or green-brown color and often a reduced marginal line; *C. n. tubensis* by reddish color and often expanded markings; *C. n. olmosa* by dark greenish brown color and expanded markings; *C. n. knausi* by reddish brown, greenish brown, green, or blue color and average markings; and *C. n. lincolniana* by dark greenish brown color and reduced markings.

In the study of geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 144); (6) width of middle band in arbitrary units (Fig. 145); (7) width of apical lunule in arbitrary units (Fig. 146); (8) color of elytra, using color wheel.

Specimens from 18 localities were measured; the localities and sample sizes are given in Table 34. Sample sizes were adequate for nearly all localities, except some in New Mexico, Utah, and Kansas.

The means for the characters and localities are given in Tables 35 and 36. Analyses of variance of the individual characters showed that there are significant differences among the means of characters 3-7 ($p < 0.01$), and character 1 ($p < 0.05$); the means of character 2 are nonsignificant for both sexes. Pooled within-locality variance-covariance matrices are given in Tables 37 and 38. The sums of the among-locality variance components are 150.835 for males and 129.146 for females. The first four components are highly significant ($p < 0.01$); and the fifth is significant at the 5% level. The first three functions account for 95.67% of the variance (among localities relative to that within) in males and 93.15% in females. The distributions of the means in the first three discriminant functions are shown in Figures 147 and 148. Localities 1, 3-11, and 18 form a fairly compact cluster, while the other localities are scattered about to varying degrees.



Figs. 144-146. Illustrations of certain characters measured on elytra of *C. nevadica*; Fig. 144, arbitrary units for shapes of base of middle band; Fig. 145, arbitrary units for width of middle band; Fig. 146, arbitrary units for width of apical lunule.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 3 vs. 8, 4 vs. 7, 4 vs. 8, 4 vs. 9, 4 vs. 10, 4 vs. 11, 5 vs. 8, 8 vs. 10, 9 vs. 11, 10 vs. 11, and 12 vs. 13 for both sexes; 4 vs. 10, 5 vs. 7, 5 vs. 10, 7 vs. 10, 9 vs. 10, and 12 vs. 15 for males; and 1 vs. 9, 3 vs. 4, 3 vs. 5, 3 vs. 7, 3 vs. 8, 3 vs. 9, 3 vs. 10, 3 vs. 11, 3 vs. 13, 7 vs. 8, 7 vs. 9, and 8 vs. 9 for females. Thus, most members of the cluster are not different from one another, but the scattered means are usually significantly different from one another and from the cluster.

Sets of vectors (Figs. 149 and 150), plotted for the first two functions, show geographic trends of the seven characters when compared with Figures 147 and 148. Specimens with high values in K_1 have a wide base of the middle band, long labrum (in males), and narrow elytra (in females); and vice versa for specimens low in K_1.

The results of the color analysis are shown in Figure 151. Specimens from California and Nevada are predominantly dark reddish (appear brown) to

TABLE 34. Localities and sample sizes of the specimens of *C. nevadica* measured.

Locality	N ♂	♀
1. MANITOBA, 6 mi. s. of Hilton	10	10
2. NEBRASKA, Lancaster Co., Lincoln (west edge)	12	12
3. KANSAS, Lincoln Co., 11 mi. n., ½ mi. e. of Lincoln	9	5
4. KANSAS, McPherson, 1.5 mi. e. of Galva	12	12
5. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
6. KANSAS, Clark Co., Englewood	12	12
7. COLORADO, Bent Co., Las Animas	12	12
8. OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	11	10
9. OKLAHOMA, Woods Co., 2.5 mi. s.w. of Plainview	12	12
10. TEXAS, Eastland Co., tank w. of Cisco	11	10
11. NEW MEXICO, Quay Co., 1 mi. n.e. of Tucumcari	12	12
12. NEW MEXICO, Taos Co., Ojo Caliente	3	4
13. NEW MEXICO, San Doval Co., 3 mi. w. of San Ysidro	4	9
14. ARIZONA, Navajo Co., 15 mi. n.n.w. of Kayenta	11	3
15. UTAH, Emery Co.	5	11
16. NEW MEXICO, Sierra Co., 25 mi. w. of Tularosa	12	8
17. NEVADA, Nye Co., Ash Meadows	12	8
18. CALIFORNIA, Kern Co., Saltdale	12	11

TABLE 35. Means of 18 localities (see Table 34) and seven characters for males of *C. nevadica*. Values for characters 1-4 are in mm.

	Character						
Locality	1	2	3	4	5	6	7
1	7.13	2.04	1.53	0.65	4.16	4.25	2.86
2	7.07	2.02	1.45	0.63	3.72	2.50	1.93
3	7.12	2.07	1.49	0.63	4.09	3.42	2.20
4	6.94	1.98	1.43	0.61	4.04	4.24	2.99
5	7.09	2.03	1.45	0.63	4.05	4.07	2.84
6	6.82	1.94	1.43	0.61	4.08	4.66	3.94
7	6.98	2.05	1.43	0.62	4.03	4.08	3.34
8	6.92	2.01	1.44	0.61	4.05	4.08	2.40
9	7.06	2.02	1.47	0.60	4.08	4.57	3.18
10	6.94	2.03	1.44	0.61	4.14	4.32	2.95
11	6.96	2.01	1.45	0.60	4.12	4.56	3.41
12	7.19	2.08	1.49	0.71	4.23	4.60	3.57
13	7.07	2.01	1.45	0.69	4.10	4.38	3.28
14	6.57	1.92	1.39	0.64	5.19	5.88	5.66
15	6.74	1.99	1.43	0.66	4.32	5.14	4.42
16	6.94	1.99	1.40	0.62	4.35	5.48	5.28
17	7.19	2.03	1.51	0.60	1.42	4.23	1.94
18	6.86	1.98	1.41	0.59	3.98	5.18	3.89

Table 36. Means of 18 localities (see Table 34) and seven characters for females of *C. nevadica*. Values for characters 1-4 are in mm.

Locality	1	2	3	Character 4	5	6	7
1	7.86	2.32	1.65	0.68	4.11	3.89	2.69
2	7.50	2.25	1.51	0.59	3.39	2.60	1.68
3	7.63	2.27	1.51	0.64	4.12	4.18	2.90
4	7.63	2.27	1.54	0.64	4.10	3.97	2.93
5	7.45	2.30	1.56	0.66	4.00	3.61	2.81
6	7.48	2.21	1.53	0.64	4.10	4.53	3.62
7	7.34	2.21	1.50	0.62	4.09	3.88	2.71
8	7.61	2.23	1.54	0.62	4.10	3.96	2.79
9	7.55	2.22	1.54	0.64	4.12	4.03	2.71
10	7.50	2.23	1.50	0.61	4.13	4.63	3.06
11	7.74	2.26	1.55	0.64	4.13	4.13	2.76
12	7.97	2.28	1.57	0.71	4.25	4.48	3.90
13	7.40	2.14	1.51	0.65	4.11	4.22	3.33
14	7.30	2.20	1.52	0.66	5.37	6.20	6.10
15	7.45	2.22	1.54	0.68	4.25	5.05	3.81
16	7.65	2.23	1.49	0.65	4.44	5.18	5.49
17	7.60	2.25	1.57	0.62	1.41	1.00	1.91
18	7.38	2.23	1.50	0.59	3.98	4.88	3.56

Table 37. Pooled within-locality variance-covariance matrix for males of *C. nevadica*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1187"=0.1187.

		1	2	3	Character 4	5	6	7
Character	1	1187	311	220	132	135	45	203
	2		108	64	39	38	29	60
	3			60	30	33	41	38
	4				24	15	22	34
	5					717	504	659
	6						2771	799
	7							3503

dark green. The Utah and Arizona samples are mostly reddish, and the northern New Mexico samples are similar, but contain many red-green individuals. The southern New Mexico population is dark red (brown) to dark-green. Other populations are quite variable in color and contain many individuals with brighter colors (in the south; northern populations are darker).

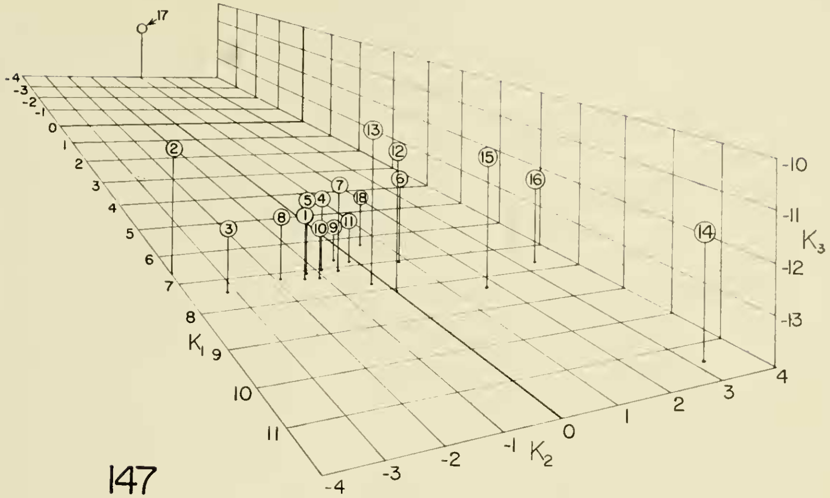
These analyses, in general, support the existence of the five subspecies. Samples representing *C. n. lincolniana* (2) and *C. n. olmosa* (16) are well

Table 38. Pooled within-locality variance-covariance matrix for females of *C. nevadica*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1198"=0.1198.

		Character						
		1	2	3	4	5	6	7
Character	1	1198	316	215	117	60	167	−26
	2		121	65	35	32	61	−13
	3			61	24	14	33	−27
	4				23	15	25	9
	5					478	321	245
	6						2101	1040
	7							2876

separated from the others in the statistical analysis. The means of *C. n. knausi* (1, 3-13) form a compact cluster. The means of *C. n. tubensis* (14 and 15) are widely separated, apparently because sample 14 contained many small, very widely maculate individuals. Localities 12 and 13 could be called intermediates between *C. n. tubensis* and *C. n. knausi* on the basis of their color. The means of *C. n. nevadica* (17 and 18) are also widely separated because most individuals in sample 17 have no marginal line, while those in 18 do, causing them to resemble *C. n. knausi* (still, 18 is significantly different from all others). However, the geographical isolation of *C. n. nevadica* and its characteristic dark color and wide transverse portion of the middle band justify its recognition. Some of the Utah specimens of *C. n. tubensis* lack the red color typical of Arizona populations, being greenish brown and thus resembling *C. n. knausi*; however, their markings average much wider than those of *C. n. knausi.* The status of the population in southeastern Arizona (if it is a valid record) is in doubt (Fig. 143). The eight specimens from there are dark green to green-brown, and have average markings with a marginal line. At present, they are being called *C. n. olmosa.* The population of "*C. n. olmosa*" from central New Mexico may be intergrades between this subspecies and *C. n. knausi*; I have seen no specimens from there.

C. nevadica almost certainly evolved in the western United States, but its range is so large, it is impossible to guess where. Its closest relatives are *C. sperata* and *C. marutha*, found in the Great Basin, northern Mexico, southern Great Plains, and (*C. sperata* only) southern Texas. The three probably evolved as the rising western mountains in late Tertiary times isolated populations of a common ancestor. *C. nevadica* then probably became widespread in the Southwest during the early Pleistocene pluvial periods, when moist climates permitted easy dispersal. During drier interglacial periods, many populations were apparently extinguished and resulting complete or partial isolation favored the development of geographic races: *C. n.*



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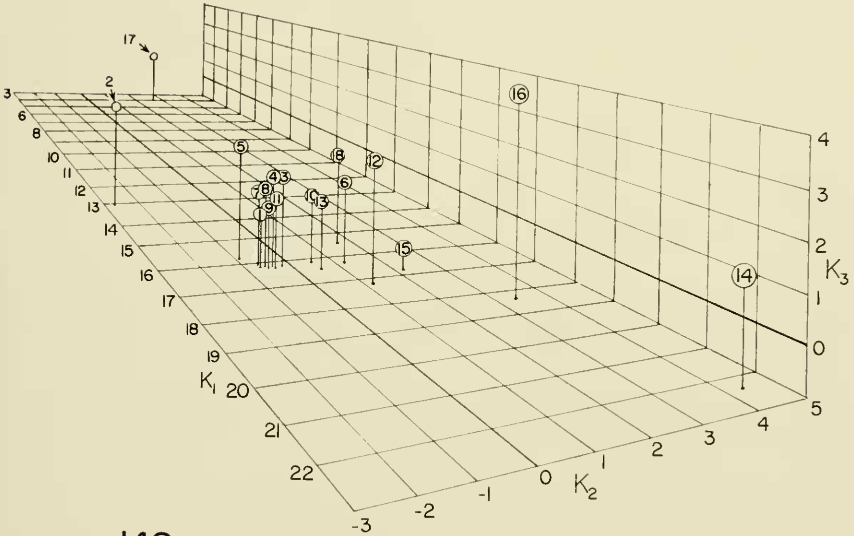

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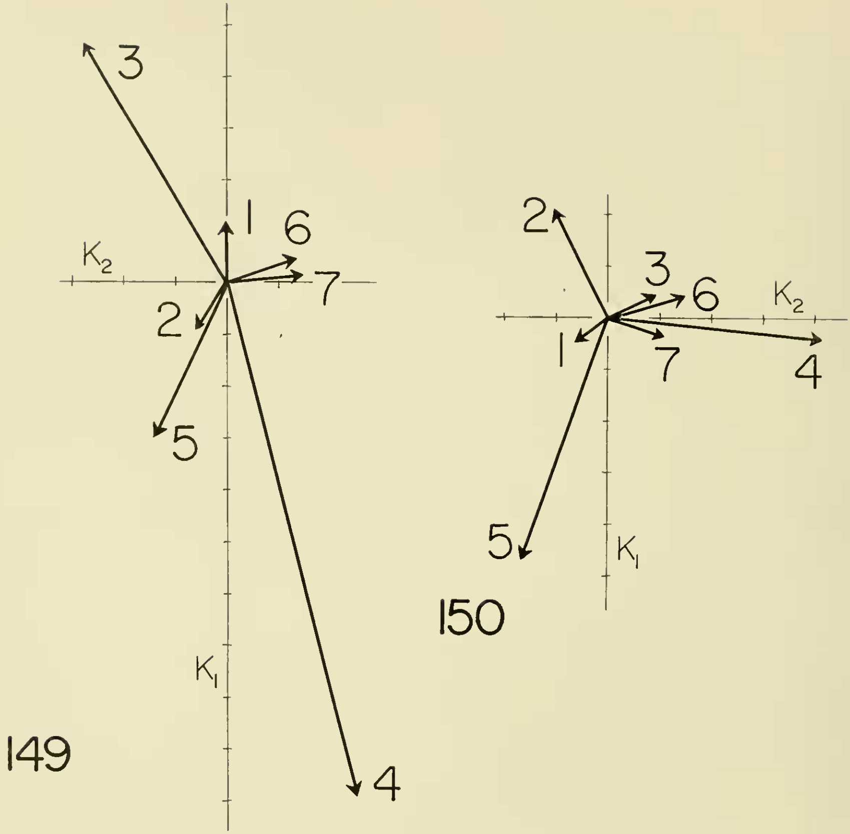
Figs. 147-148. Distributions of the means of the 18 localities for males (Fig. 147) and females (Fig. 148) of *C. nevadica* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer.

nevadica in the western Great Basin and *C. n. tubensis* on the Colorado Plateau, where it developed a red dorsal color because of the red soils in that region (Fig. 108). A third form (or ancestors of *C. n. tubensis*) spread



Figs. 149-150. Vectors for the seven characters of males (Fig. 149) and females (Fig. 150) of *C. nevadica* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 147-148.

throughout the region drained by the Rio Grande and Pecos River; those along the lower Rio Grande became *C. n. olmosa*, while the others *(C. n. knausi)* dispersed northeastward. Glaciations evidently pushed *C. n. knausi* as far south as central Texas, where a relict population still exists in Eastland County. *C. n. knausi* probably reached the Lincoln, Nebraska, vicinity sometime after the Kansan glaciation, probably during the Yarmouth. From then on, it was apparently isolated from the rest of the gene pool and evolved into *C. n. lincolniana.* After the Wisconsin glaciation, *C. n. knausi* quickly dispersed northward into the Dakotas, Montana, and southern Canada. The fact that *C. n. knausi* has not developed completely reddish populations in western Oklahoma indicates that it has not been in this area as long as *C. n. tubensis* has been on the Colorado Plateau; however, the Oklahoma popula-

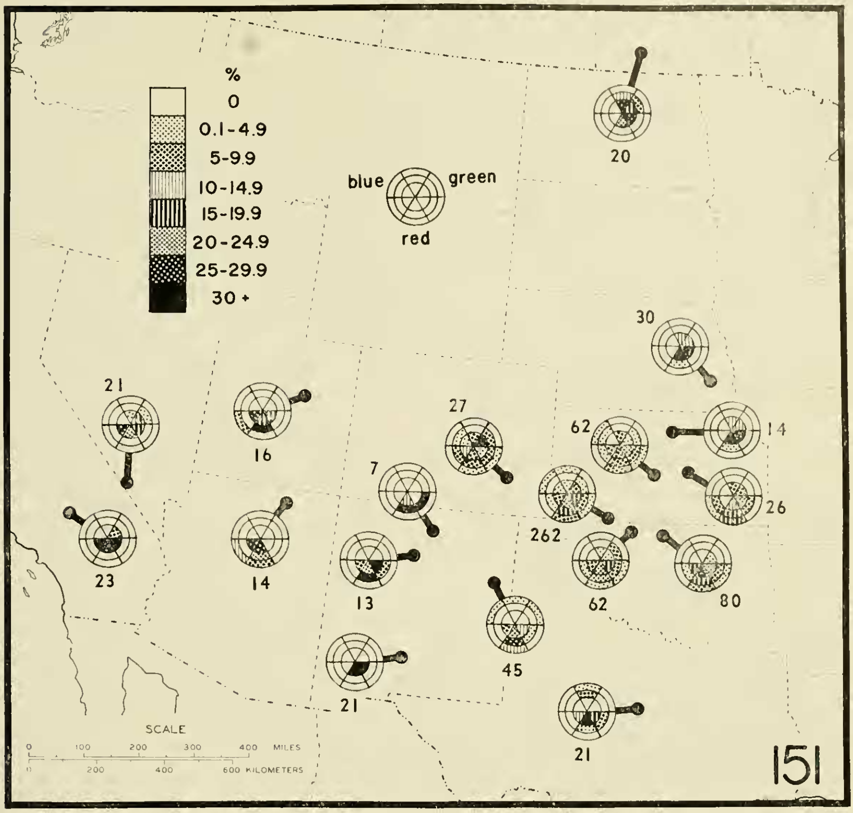


Fig. 151. Results of color analysis of *C. nevadica* using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three majors colors are shown at top center. Numbers show the sample size for each locality.

tions seem to be evolving in that direction, because they contain many bright red individuals, compared to populations from north of there (Fig. 151).

C. togata

This is a southern species found along the Gulf and Atlantic coasts from South Carolina to northern Mexico, and inland from western Texas to Nebraska (Fig. 152). Its distribution by counties or states is as follows:

NEBRASKA: Dodge, Fillmore, Lancaster, Nuckolls, Saunders; COLORADO: Chaffee, Otero; KANSAS: Barber, Butler, Clark, Cloud, Kiowa, Lincoln, McPherson, Mitchell, Reno, Republic, Sedgwick, Stafford; OKLAHOMA: Alfalfa, Beckham, Blaine, Garfield, Grant, Harmon, Harper, Jackson, Logan, Muskogee, Woods; NEW MEXICO: Chaves, Eddy, Guadalupe, Torrance; TEXAS: Andrews, Aransas, Bailey, Brazoria, Calhoun, Cameron, Childress, Dallas, Dawson, Dimmet, El Paso, Gaines, Galveston, Harris, Hidalgo, Hudspeth, Jackson, Jefferson, Kenedy, Kleberg, Live Oak, Matagorda, Mitchell, Nueces, Reeves, San Patricio, Val Verde, Wichita, Wilbarger; TAMAULIPAS; LOUISIANA: Cameron; ALABAMA: Mobile; FLOR-

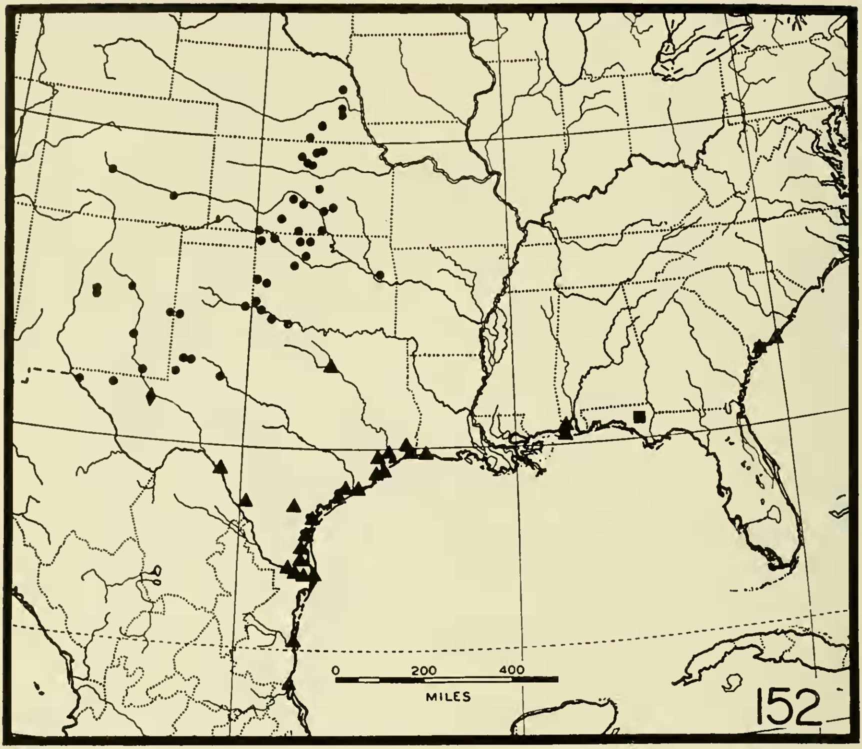


Fig. 152. Known distribution of *C. togata.* Triangle=*C. t. togata*, circle=*C. t. globicollis*, diamond=intergrade population, square=state record.

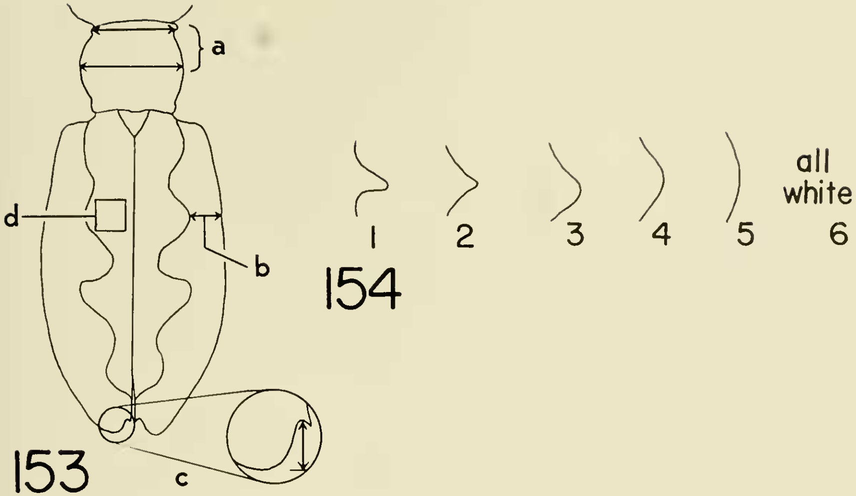
IDA; SOUTH CAROLINA: Beaufort, Charleston. The town of Meredith, South Carolina, could not be located. Saltair, Utah, is a doubtful record.

The following forms have been described within this species:

Cicindela togata LaFerté, 1841. Type locality: Texas.
Cicindela togata latilabris, new name for *Cicindela togata apicalis* W. Horn, 1897 (not *apicalis* Chaudoir, 1843). Type locality: Nebraska, Kackley (misspelled "Kakley"), Kansas. Preoccupied.
Cicindela globicollis Casey, 1913. Type locality: Clark County, Kansas.
Cicindela fascinans Casey, 1914. Type locality: Santa Rosa, New Mexico.

In recent years, three subspecies have been recognized: *C. t. togata*, the rather small coastal form with the apical elytral spine of the female greatly retracted; *C. t. globicollis*, the large northern form with the apical elytral spine of the female slightly retracted; and *C. t. fascinans*, the small southwestern form with expanded markings and slightly retracted apical elytral spine in the female.

The following characters were measured in the study of geographic variation: (1) width of head; (2) width of pronotum at widest point; (3)



Figs. 153-154. Illustrations of certain characters measured on *C. togata*; Fig. 153: a=pronotal bulge, b=width of maculation, c=retraction of elytral spine of female, d=number of punctures in 0.45 m^2 area at this position; Fig. 154, arbitrary units for shape of middle band.

"pronotal bulge," the difference between character 2 and the width of the pronotum at its anterior margin (Fig. 153a); (4) width of left elytron; (5) length of left elytron; (6) width of maculation at a specified place (Fig. 153b); (7) retraction of left apical elytral spine (distance from its base to apex of elytron) of female (Fig. 153c); not measurable in males because the spine is truly apical; (8) number of punctures in a 0.45 mm^2 square on a specified part of the left elytron (Fig. 153d); (9) average width of setae on center of pronotum; (10) shape of middle band in arbitrary units (Fig. 154); (11) color of elytra in arbitrary units: 1=dark green-brown, 2=dark green-cupreous, 3=green-cupreous, 4=cupreous, 5=dark purplish cupreous, 6=dark green-purple; (12) length of labrum, excluding tooth; (13) width of labrum.

Specimens from 19 localities were measured; the localities and sample sizes are given in Table 39. Sample sizes were adequate except for localities in the southwestern part of the range and from Dallas, Texas. Specimens from New Mexico were lumped into one sample.

The means for the characters and localities are given in Tables 40 and 41. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters. Pooled within-locality variance-covariance matrices are given in Tables 42 and 43. The sums of the among-locality variance components are 258.487 for males and 284.879 for females. The first eight components for males and the first five for females are highly significant ($p < 0.01$), and the sixth component

Table 39. Localities and sample sizes of the specimens of *C. togata* measured.

Locality	N ♂	N ♀
1. NEBRASKA, Lancaster Co., Lincoln (west edge)	10	10
2. KANSAS, Republic Co., ½ mi. e., 1 s. of Talmo	10	10
3. KANSAS, Lincoln Co., 3 mi. w., 2 s. of Barnard	10	10
4. KANSAS, Butler Co., El Dorado (west edge)	10	10
5. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	10	10
6. KANSAS, Clark Co., Englewood	10	10
7. OKLAHOMA, Alfalfa Co., 3 mi. e. of Cherokee	10	10
8. OKLAHOMA, Garfield Co., ½ mi. n.w. of Drummond	10	10
9. OKLAHOMA, Jackson Co., 3.5 mi. s. of Eldorado	10	10
10. TEXAS, Bailey Co., 9 mi. s., 9 w. of Muleshoe (Coyote L.); NEW MEXICO, Roosevelt Co., 4 mi. e., 1 s. of Arch	4	5
11. TEXAS, Andrews Co., 8 mi. n.w., 3.5 mi. s.w. of Andrews (Shafter L.)	9	10
12. NEW MEXICO, Chaves Co., 8 mi. n.e. of Roswell; Eddy Co., 6 mi. e., 2 n. of Loving	6	1
13. TEXAS, Hudspeth Co.. 90 mi. e. of El Paso (near Salt Flat)	7	2
14. TEXAS, Val Verde Co., Del Rio	10	10
15. TEXAS, Dallas Co., Dallas	1	3
16. TEXAS, Kleberg Co., Riviera Beach	10	10
17. TEXAS, Galveston Co., Galveston	10	10
18. ALABAMA, Mobile Co., Coden	10	10
19. SOUTH CAROLINA, Charleston Co., Folly Beach	10	10

Table 40. Means of 19 localities (see Table 39) and 12 characters for males of *C. togata*. Values for characters 1-6, 9, 12, and 13 are in mm.

	Character											
	1	2	3	4	5	6	8	9	10	11	12	13
1	3.04	2.40	0.44	2.01	7.46	0.54	63.0	0.0190	1.29	1.25	0.76	1.47
2	3.21	2.44	0.43	2.04	7.51	0.59	60.1	0.0196	1.42	1.57	0.75	1.49
3	2.92	2.23	0.37	1.92	7.02	0.64	63.4	0.0180	2.34	2.42	0.74	1.37
4	3.09	2.41	0.44	2.02	7.39	0.66	57.8	0.0164	1.81	3.65	0.72	1.47
5	3.11	2.40	0.38	2.03	7.41	0.78	64.0	0.0200	2.77	3.06	0.74	1.47
6	2.93	2.25	0.40	1.90	6.78	0.77	60.1	0.0194	3.03	3.85	0.72	1.36
7	2.97	2.28	0.38	1.90	7.07	0.72	64.8	0.0190	2.53	4.19	0.69	1.41
8	3.09	2.36	0.43	2.00	7.37	0.71	56.2	0.0194	2.49	4.44	0.75	1.46
9	3.21	2.41	0.42	2.00	7.21	0.89	56.2	0.0210	3.35	4.40	0.75	1.47
10	3.10	2.42	0.38	1.96	7.26	0.83	54.2	0.0235	2.45	4.38	0.79	1.49
11	3.09	2.41	0.38	2.01	7.33	1.01	51.9	0.0227	4.01	4.30	0.79	1.53
12	2.72	2.01	0.32	1.69	6.40	0.81	63.3	0.0235	3.57	4.02	0.65	1.28
13	3.03	2.17	0.34	1.88	6.66	1.88	53.3	0.0239	6.00	4.14	0.79	1.37
14	2.95	2.17	0.36	1.86	6.77	0.62	55.5	0.0200	2.85	4.77	0.71	1.33
15	2.82	1.95	0.21	1.74	6.25	0.61	61.0	0.0220	3.60	4.60	0.65	1.26
16	3.10	2.29	0.40	1.95	6.86	0.72	55.1	0.0225	3.28	4.69	0.74	1.36
17	3.06	2.20	0.32	1.93	6.84	0.67	55.2	0.0191	2.77	4.80	0.72	1.35
18	2.83	1.96	0.27	1.81	6.38	0.70	54.7	0.0186	2.77	4.78	0.65	1.24
19	3.06	2.19	0.32	1.87	6.84	0.71	55.2	0.0175	1.51	4.89	0.72	1.34

Table 41. Means of 19 localities (see Table 39) and 13 characters for females of *C. togata*. Values for characters 1-7, 9, 12, and 13 are in mm.

	Character												
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13
1	3.33	2.63	0.41	2.31	8.23	0.66	0.14	56.1	0.0188	1.17	1.53	0.80	1.60
2	3.49	2.63	0.38	2.31	8.25	0.59	0.16	55.4	0.0201	1.23	1.44	0.81	1.60
3	3.15	2.39	0.34	2.06	7.48	0.57	0.10	58.9	0.0172	1.41	2.32	0.71	1.44
4	3.24	2.45	0.38	2.12	7.57	0.62	0.13	53.3	0.0178	2.09	3.82	0.74	1.46
5	3.26	2.51	0.35	2.21	7.83	0.76	0.11	57.4	0.0208	2.38	2.83	0.78	1.55
6	3.07	2.32	0.36	2.05	7.08	0.75	0.11	59.9	0.0198	2.67	3.71	0.74	1.39
7	3.19	2.40	0.33	2.11	7.70	0.71	0.11	57.3	0.0193	1.97	3.61	0.76	1.49
8	3.43	2.59	0.40	2.24	8.01	0.70	0.18	50.9	0.0205	1.80	3.52	0.80	1.57
9	3.22	2.37	0.34	2.07	7.32	0.74	0.14	55.5	0.0210	2.07	4.41	0.75	1.45
10	3.36	2.61	0.41	2.33	7.99	0.87	0.14	50.8	0.0252	2.28	3.88	0.86	1.59
11	3.24	2.48	0.34	2.18	7.65	0.92	0.12	51.5	0.0213	3.16	3.88	0.82	1.58
12	3.38	2.51	0.36	2.20	7.89	1.18	0.10	54.0	0.0230	3.00	3.90	0.86	1.57
13	3.10	2.10	0.28	1.97	6.86	1.97	0.11	55.5	0.0240	6.00	4.20	0.83	1.35
14	3.29	2.37	0.33	2.11	7.31	0.68	0.39	51.8	0.0211	3.01	4.82	0.77	1.47
15	3.23	2.27	0.32	2.07	7.25	0.77	0.36	48.7	0.0207	3.07	4.70	0.73	1.38
16	3.30	2.42	0.34	2.08	7.33	0.74	0.42	49.2	0.0239	2.82	4.71	0.76	1.43
17	3.32	2.28	0.29	2.11	7.34	0.69	0.44	51.8	0.0197	1.70	4.96	0.77	1.45
18	3.08	2.13	0.27	2.01	6.80	0.75	0.30	50.5	0.0176	2.15	4.71	0.70	1.35
19	3.22	2.24	0.30	1.98	7.02	0.67	0.30	54.0	0.0176	1.37	4.87	0.75	1.39

Table 42. Pooled within-locality variance-covariance matrix for males of *C. togata*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "186"=0.0186.

	Character											
Character	1	2	3	4	5	6	8	9	10	11	12	13
1	186	146	14	102	407	72	−2690	1	89	13	52	81
2		156	32	91	375	70	−2773	0	129	18	47	72
3			27	10	36	9	−344	0	28	−13	6	7
4				93	294	53	−1957	0	91	31	36	51
5					1345	193	−7617	1	315	100	141	213
6						104	−1594	0	229	29	22	34
8							228105	−9	−1602	−571	−1000	−1442
9								0	1	−0	0	0
10									3449	225	34	52
11										1684	−3	22
12											24	26
13												47

for females is significant at the 5% level. The first three functions account for 87.95% of the variance (among localities relative to that within) in males and 88.96% in females. The distributions of the means in the first three discriminant functions are shown in Figures 155 and 156. Localities 14-19 form a fairly compact cluster, while the others are scattered in a loose cluster, except 13, which is widely separated.

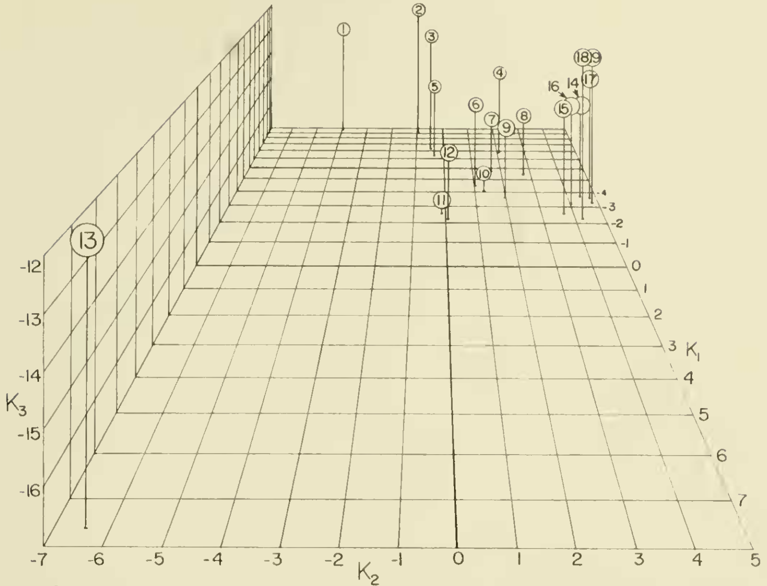
The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 15 vs. 16 and 15 vs. 18 for both sexes; 15 vs. 6, 15 vs. 9, 15 vs. 10, 15 vs. 12, 15 vs. 14, 15 vs. 17, and 15 vs. 19 for males; and 4 vs. 8, 5 vs. 7, 6 vs. 12, 9 vs. 12, 10 vs. 12, 11 vs. 12, and 14 vs. 15 for females. The low sample size of one individual for males from locality 15 and of females from locality 12 accounts for the many nonsignificant pairs involving those localities.

Sets of vectors (Figs. 157 and 158), plotted for the first two functions, show geographic trends of the characters when compared with Figures 155 and 156. Specimens with high values in K_1 (southwestern localities) have wide maculation, a long labrum, a greater pronotal bulge, and (in males) wider pronotal setae. Specimens low in K_1 and K_2 (northern localities) have a wide labrum, narrow head, and low arbitrary color values. Specimens low in K_1 and high in K_2 (coastal localities) have a wide head, a narrow labrum, high color values, and (in females) wide pronotal setae and a more greatly retracted elytral spine.

The pattern of variation of four of these characters is shown in Figure 159. The width of maculation shows a gradual increase from northeast to southwest, while all coastal and eastern Texas samples have narrow maculation. The same general pattern is shown by the width of pronotal setae, although some eastern Texas samples have very high values. Arbitrary color values increase from northeast to southwest, thence to the southeast. The retraction

Table 43. Pooled within-locality variance-covariance matrix for females of *C. togata*. Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "268"=0.0268.

	Character												
Character	1	2	3	4	5	6	7	8	9	10	11	12	13
1	268	181	30	152	571	74	21	−2681	0	111	7	62	117
2		202	49	120	439	59	8	−1858	1	104	−5	45	90
3			38	21	72	6	−1	−7	0	−3	−21	7	14
4				132	379	54	13	−2015	0	91	28	40	76
5					1590	211	53	−7603	1	344	115	154	273
6						94	12	−910	1	218	13	21	39
7							18	−87	−0	26	8	7	9
8								226118	−0	−2788	1153	−840	−1483
9									0	1	−0	0	0
10										2310	13	47	66
11											2379	−14	25
12												27	31
13													65



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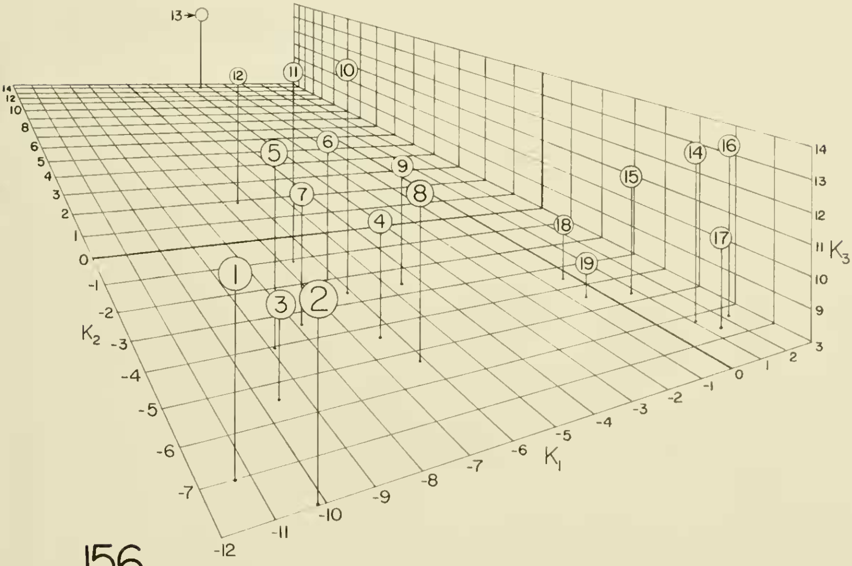

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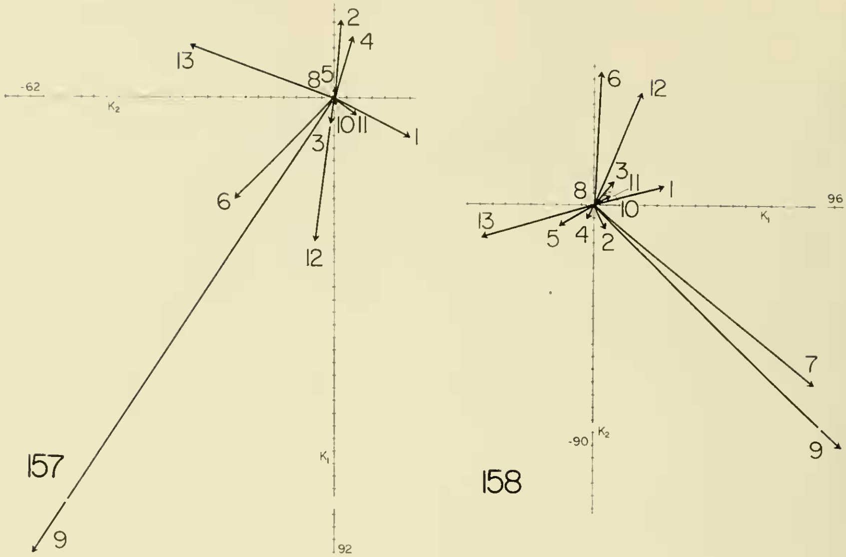
Figs. 155-156. Distributions of the means of the 19 localities for males (Fig. 155) and females (Fig. 156) of *C. togata* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.



FIGS. 157-158. Vectors for the 12 characters of males (Fig. 157) and 13 of females (Fig. 158) of *C. togata* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 155-156.

of the female elytral spine is small in all northwestern samples and great in southeastern samples.

The pattern of variation is complicated by specimens not measured from localities in west-central Texas. Three out of four specimens before me from Sand, Dawson County, Texas, are small and with completely white elytra (like specimens from locality 13 in Hudspeth County, Texas); the fourth is larger and similar to specimens from east-central New Mexico or southwestern Oklahoma. Of six specimens from Potash Lake, Gaines County, Texas, one has very wide markings, with only a narrow sutural band of the elytra not white; the others are more "normal."

Another characteristic of many southwestern populations of this species is the occurrence of occasional individuals with elytral basal dots (Fig. 91). Sometimes the dots are quite large and connect to the marginal maculation, but usually they are poorly developed and isolated. This has been noted in most samples from New Mexico, western Texas, and southwestern Oklahoma; and it even occurs as far northeast as southwestern Kansas and El Dorado, in east-central Kansas.

A clear division of the localities into two groups is shown in the above analysis, a coastal and eastern Texas form, *C. t. togata*, best characterized by the great retraction of the female elytral spine; and the northwestern populations, in which this spine is only slightly retracted. Within the latter group,

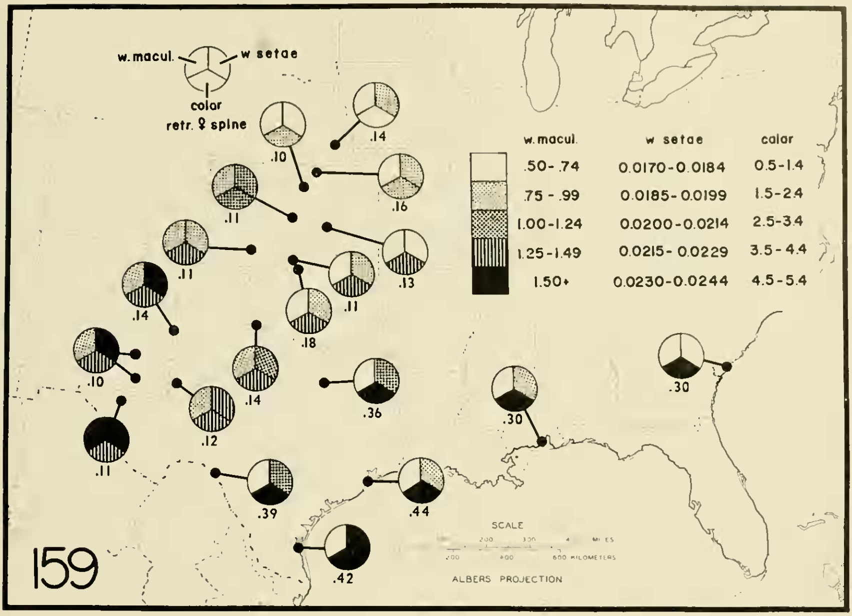


Fig. 159. Geographic variation of four characters of *C. togata*: width of the maculation, width of pronotal setae, color, and retraction of the elytral spine of the female. Values for the first three characters have been pooled for the sexes and represented by different degrees of shading (upper right). Values for the fourth character are beneath each circle. The positions of the characters in the circles are shown at upper left.

a gradual cline exists in most characters measured, running from northeast to southwest, with no clear breaks or steps (or at least none in which there is any sort of character concordance). The type localities of the two valid named forms in this group are Clark County, Kansas, and Santa Rosa, New Mexico. Specimens from these areas are more similar to one another than are those from northern Kansas and Clark County or those from western Texas and Santa Rosa. Thus, only the earlier of these two names, *C. t. globicollis*, should be used. The form with completely white elytra from Hudspeth County, Texas, is certainly distinct enough to be called a subspecies, but as noted above, some specimens from west-central Texas are identical to or closely approach it; and intervening populations are more nearly "normal." Therefore, it does not seem advisable to recognize more than two subspecies within this species (Fig. 152). The two (female) specimens that I have seen from Pecos, Reeves County, Texas, appear to be intermediate between the two subspecies. One has a greatly retracted elytral spine and is greenish. The other has a slightly retracted spine and is cupreous. The maculation is fairly wide in both specimens.

C. togata probably evolved within its present range. It has no close relatives, so it is difficult to say whether it was first a coastal or an inland species. It eventually became widespread, evidently, in both coastal and inland habitats in the southern United States. Differentiation into races probably began in the form of a cline along the Rio Grande valley. The drier climates of late Tertiary or interglacial Pleistocene times no doubt exterminated many of the intermediate populations of the cline, resulting in evolution into the modern coastal and inland subspecies. Dispersal of the inland form to the northeast probably occurred during the Pleistocene. It could not have reached the Lincoln, Nebraska, area until after the Nebraskan glaciation.

The pattern of maculation and color variation seem clearly to be a result of selection to match the substrate color. In the drier Southwest, where saline habitats are more often covered by a white crust of salt, the width of the maculation is greatest. Populations with color values around 4 (cupreous) are found in the area with red soil (Figs. 159 and 108). Dark soils are prevalent in most other areas, and the beetles there are also dark. In some southwestern habitats, however, the soil is light gray, nearly white. Here, the elytra of *C. togata* are completely white or nearly so. The presence of the basal dot seems to be evolving in southwestern populations; it has the effect of increasing the amount of white on the elytra. Increased width of body setae also has the effect of making the beetle appear more white, a trend that has been noted in southwestern populations.

C. willistoni

This is a western species, most common in the Great Basin and Mojave Desert, and reaching its eastern limit in Kansas and Oklahoma (Fig. 160). Its distribution by county or state is the following:

KANSAS: Stafford; OKLAHOMA: Alfalfa, Beckham, Woods; TEXAS: Andrews; NEW MEXICO: Roosevelt, Torrance, Valencia; WYOMING: Albany, Carbon, Uinta; UTAH: Beaver, Box Elder, Cache, Davis, Emery-Rand County line, Iron, Juab, Millard, Salt Lake, Tooele, Utah, Washington; ARIZONA; NEVADA: Churchill, Lyon, Nye, Storey, Washoe; CALIFORNIA: Alameda, Inyo, Kern, Lassen, Los Angeles, Orange, Plumas, San Bernardino; OREGON: Harney, Lake. Town that could not be located: Farr Post (=Farrwest, Weber County ?), Utah. *Doubtful localities:* Kellwood, Manitoba; Colorado Springs, El Paso County, Colorado. The Los Angeles County (Seal Beach), Alameda Co. and Orange Co. (Irvine), California, localities (listed above) are somewhat questionable.

The following forms have been described within this species:

Cicindela willistoni Leconte, 1879. Type locality: Lake Como, Wyoming Territory.

Cicindela echo Casey, 1897. Type locality: Great Salt Lake, Utah.

Cicindela pseudosenilis W. Horn, 1900. Type locality: Owens Lake, Inyo County, California.

Cicindela echo amedeensis (emendation of *C. e. amadeensis* Casey, 1909). Type locality: Amedee, California. This form is clearly named for the type locality, but in the original description, the name is apparently misspelled.

Cicindela spaldingi Casey, 1924. Type locality: Callao, Utah.

Cicindela willistoni amargosae Dahl, 1939. Type locality: 4 miles north of Furnace Creek, Inyo County, California. This form is now recognized as a separate species.

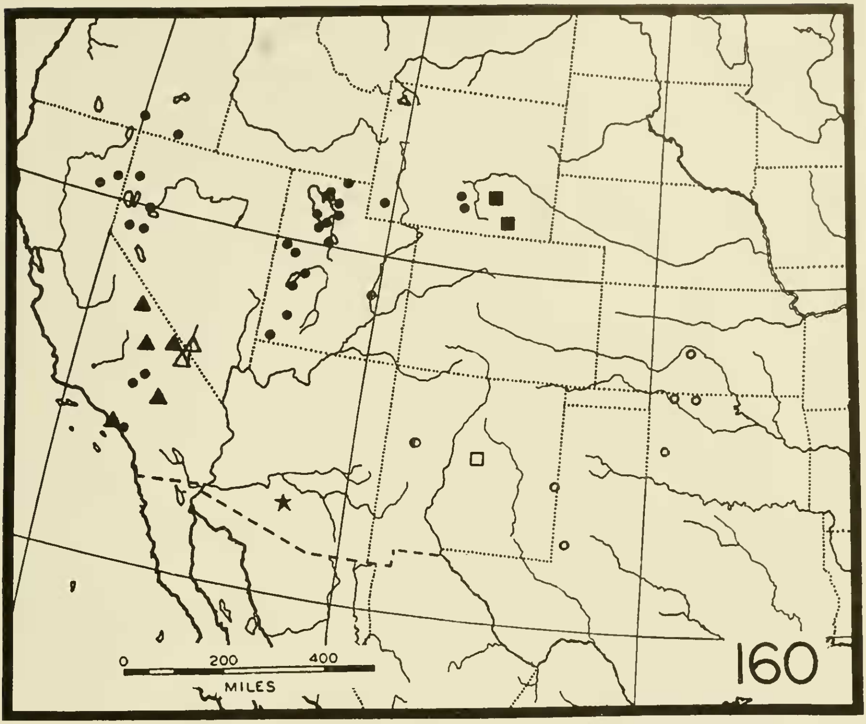


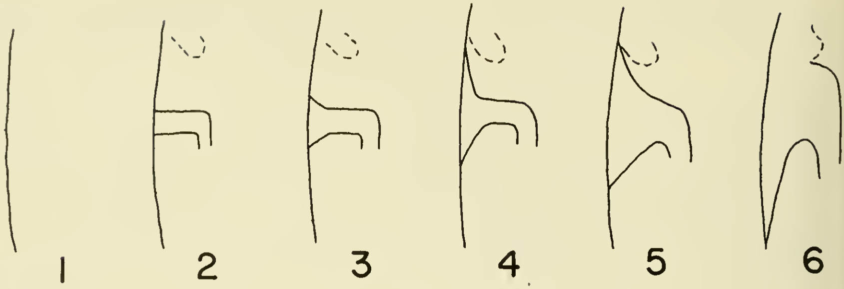
Fig. 160. Known distribution of *C. willistoni*. Shaded square=*C. w. willistoni*, shaded circle=*C. w. echo*, shaded triangle=*C. w. pseudosenilis*, open triangle=*C. w. praedicta*, open square=*C. w. estancia*, open circle=*C. w. hirtifrons*, half shaded circle=population of uncertain status, star=state record.

Cicindela willistoni praedicta Rumpp, 1956. Type locality: 3.5 miles south of Shoshone, Inyo County, California.

Cicindela willistoni estancia Rumpp, 1961. Type locality: 7 miles east of Willard, Torrance County, New Mexico.

In recent years, five subspecies have been recognized: *C. w. willistoni*, the reddish brown form with marginally expanded markings; *C. w. echo*, the brownish form with usually "average" markings; *C. w. pseudosenilis*, the blue or blue-green form, sometimes with expanded markings; *C. w. praedicta*, the small blue or blue-green form with reduced markings or none at all; and *C. w. estancia*, the feddish brown form with markings so expanded, the elytra are nearly completely white.

In the study of geographic variation, the following characters were measured: (1) length of left elytron; (2) width of left elytron; (3) width of labrum; (4) length of labrum, including tooth; (5) shape of base of middle band in arbitrary units (Fig. 161); (6) smallest width of transverse portion of middle band (Fig. 162); (7) number of setae on vertex and frons, except



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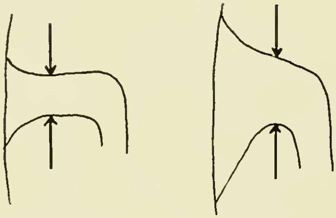

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Figs. 161-162. Illustrations of certain characters measured on elytra of *C. willistoni*; Fig. 161, arbitrary units for shape of base of middle band; Fig. 162, smallest width of transverse portion of middle band.

the several supraorbital sensory setae near the medial margins of the eyes; (8) color, using color wheel.

Specimens from seven localities were measured. The localities and sample sizes are given in Table 44. Sample sizes are adequate except for females from Oregon (specimens from Oregon were lumped into one sample) and Kern County, California. Unfortunately, these seven localities do not encompass all the recognized forms mentioned above; no specimens of *C. w. estancia* were available.

The means for the characters and localities are given in Tables 45 and 46. Analyses of variance of the individual characters showed that there are significant differences ($p < 0.01$) among the means of all characters in males and all characters in females except number 1, which is significant at the 5% level. Pooled within-locality variance-covariance matrices are given in Tables 47 and 48. The sums of the among-locality variance components are 218.88 for males and 429.67 for females. The first four components for males and the first three for females are highly significant ($p < 0.01$), and the fourth component for females is significant at the 5% level. The first three functions account for 96.66% of the variance (among localities relative to that within)

Table 44. Localities and sample sizes of the specimens of *C. willistoni* measured.

Locality	N ♂	N ♀
1. KANSAS, Stafford Co., 11 mi. n.e. of Hudson	12	12
2. WYOMING, Carbon Co., Como Lake	12	12
3. UTAH, Salt Lake Co., vicinity of Salt Lake City and Saltair	12	12
4. OREGON, Lake Co., Rest Lake, Summer Lake; Harney Co., Alvord Hot Springs	8	3
5. CALIFORNIA, Inyo Co., Olancho (Owens L.)	12	12
6. CALIFORNIA, Kern Co., Saltdale	12	4
7. CALIFORNIA, Inyo Co., 3.5 mi. s. of Shoshone	12	12

Table 45. Means of seven localities (see Table 44) and seven characters for males of *C. willistoni*. Values for characters 1-4 are in mm.

Locality	Character 1	2	3	4	5	6	7
1	7.61	2.31	1.82	0.93	3.98	0.59	31.0
2	7.66	2.39	1.82	0.94	6.09	1.38	22.2
3	7.51	2.31	1.74	0.81	4.18	0.80	5.7
4	7.96	2.39	1.87	0.88	3.75	0.85	5.6
5	7.69	2.30	1.82	0.88	3.50	0.86	6.2
6	7.63	2.33	1.81	0.88	4.79	1.15	4.8
7	7.96	2.03	1.63	0.79	1.37	0.15	5.2

Table 46. Means of seven localities (see Table 44) and seven characters for females of *C. willistoni*. Values for characters 1-4 are in mm.

Locality	Character 1	2	3	4	5	6	7
1	7.84	2.59	1.84	0.96	4.01	0.56	38.3
2	7.84	2.64	1.85	1.00	5.99	1.28	28.6
3	7.64	2.53	1.81	0.86	3.54	0.79	6.8
4	7.58	2.46	1.80	0.89	3.63	0.74	6.3
5	7.80	2.50	1.85	0.91	2.88	0.77	5.8
6	7.82	2.56	1.87	0.92	4.98	1.23	5.3
7	7.33	2.26	1.70	0.85	1.00	0.00	5.8

in males and 98.80% in females. The distributions of the means in the first three discriminant functions are shown in Figures 163 and 164. Localities 3-6 form a loose cluster (especially in males), while the others are widely scattered.

The results of the simultaneous testing procedure show that all combinations of pairs of means are significantly different at the 5% level except 4 vs. 5 for males and 3 vs. 4 for females.

TABLE 47. Pooled within-locality variance-covariance matrix for males of *C. willistoni.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1082"=0.1082.

					Character			
		1	2	3	4	5	6	7
Character	1	1082	286	246	148	540	224	1582
	2		106	72	43	205	80	391
	3			69	40	113	63	427
	4				31	90	36	103
	5					2521	580	−474
	6						341	−508
	7							184355

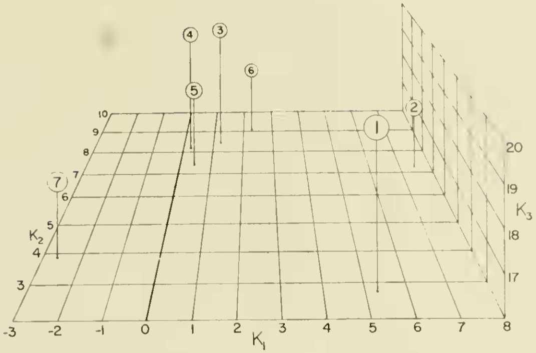
TABLE 48. Pooled within-locality variance-covariance matrix for females of *C. willistoni.* Variances are along the diagonal, and covariances compose the rest of the matrix. Values have been multiplied by 10^{-4}; thus "1748"=0.1748.

					Character			
		1	2	3	4	5	6	7
Character	1	1748	569	394	268	208	189	−2314
	2		235	136	93	45	58	−523
	3			105	67	64	41	−462
	4				50	39	28	−361
	5					1060	219	1186
	6						183	−681
	7							193125

Sets of vectors (Figs. 165 and 166), plotted for the first two functions, show geographic trends of the seven characters when compared with Figures 163 and 164. Specimens with high values in K_2 and low values in K_1 (localities 1 and 2) have a long, narrow labrum, while specimens from other localities have wider labra. Specimens low in K_1 and K_2 (locality 7) have long elytra and narrow markings, while specimens high in K_2 (localities 3-6) have wide elytra and broad markings.

The results of the color analysis are shown in Figure 167. Samples from Oregon and Utah consist mostly of dark purplish to dark red-green (appears brown-green) individuals. The southwesternmost sample in California is similar but contains many green individuals. The other two California samples contain mostly blue to blue-green individuals. The samples from Wyoming and Kansas contain many individuals with brighter colors, ranging from purplish to reddish to red-green (and green in Wyoming).

These analyses confirm the existence of four of the above five recognized subspecies (the fifth, *C. w. estancia*, is clearly distinct because of its extremely wide markings). Localities 2 *(C. w. willistoni)* and 7 *(C. w. praedicta)* are



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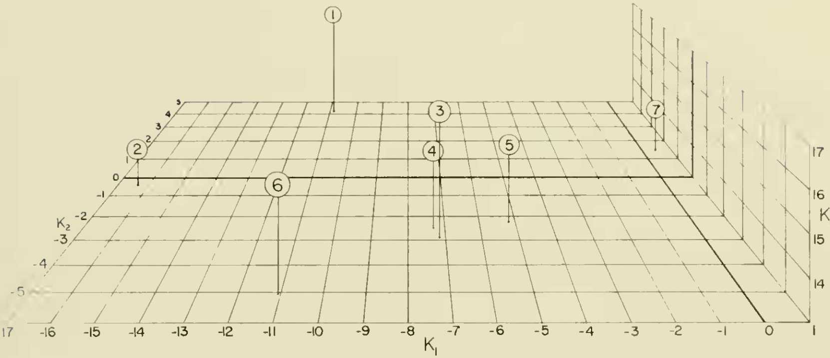

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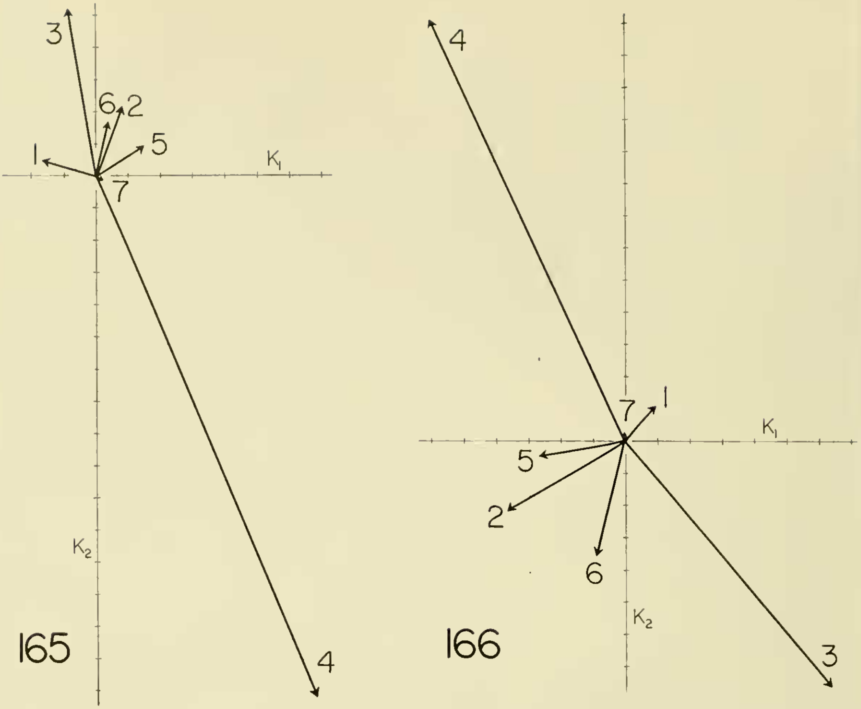
Figs. 163-164. Distributions of the means of the seven localities for males (Fig. 163) and females (Fig. 164) of *C. willistoni* in the first three discriminant functions (K_1, K_2, K_3), drawn as three-dimensional models, with numbered balls representing the means and vertical supports arising from the K_1, K_2 surface. Different sized balls indicate different distances from the viewer. The models are viewed from opposite directions, relative to the clusters.

widely separate from all other in the statistical analysis. Locality 5 *(C. w. pseudosenilis)* is quite similar to localities 3, 4, and 6 *(C. w. echo)* except in color. Specimens from Kern County, California (locality 6, Saltdale, also Mojave) differ from other populations of *C. w. echo* in having the middle band nearly always very wide in the transverse portion, sometimes broadly confluent with the humeral lunule. In other populations of *C. w. echo*, only occasional individuals exhibit this tendency. Also many (about 17%) of the Kern County specimens are dark green or blue-green. On the basis of these characters and their geographical isolation, they could probably be separated as a subspecies, although this will not be done at present. The Kansas sample



Figs. 165-166. Vectors for the seven characters of males (Fig. 165) and females (Fig. 166) of *C. willistoni* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would produce if it varied independently. Units are same as in Figs. 163-164.

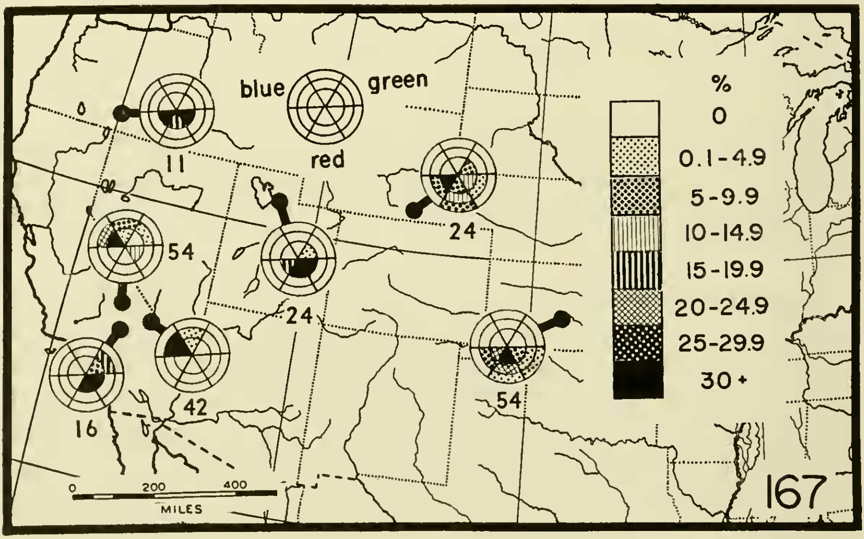


Fig. 167. Result of color analysis of *C. willistoni*, using the color wheel. Different degrees of shading indicate different percentages of the sample. The positions of the three major colors are shown at top center. Numbers show the sample size for each locality.

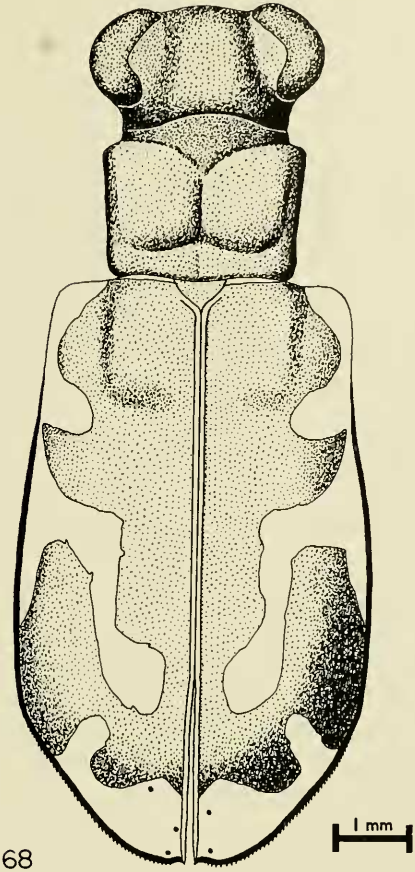


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Fig. 168. *Cicindela willistoni hirtifrons,* new subspecies; dorsal aspect of male (setae omitted).

was widely separated from the others by the statistical analysis; it represents what seems to be a clearly defined new subspecies, described below:

Cicindela willistoni hirtifrons, new subspecies (Fig. 168)

Head: Labrum with single median tooth, length usually more than half the width; antennal scape with 10-25 stout erect setae; clypeus and genae glabrous; frons and vertex with 16-51 fine erect setae medially, some long, some short (not including several pairs of sensory setae near medial margins of eyes); *Thorax:* pronotum glabrous medially, with long, erect to partly decumbent setae laterally; proepisternum, proepimeron, procoxae, mesepimeron, mesocoxae, metaepisternum, and lateral parts of metaepisternum and metacoxae with dense, long to medium erect setae; mesepisternum with a few erect setae; mesosternum and medial portions of metasternum and metacoxae with sparse short setae; prosternum glabrous; lateral margins of pronotum subparallel, diverging slightly anteriorly; *Abdomen:* venter with dense to sparse decumbent to erect setae; *Elytra:* male, gradually widened to one-half to two-thirds their length, then gradually narrowed to apical fifth, then abruptly narrow to rounded apex; female, margins much expanded at middle from basal fourth to apical third, then rounded to apex; posterior margin microserrulate; spine apical to slightly retracted; markings similar to those of typical *C. w. echo*, but middle band often narrower; humeral lunule and middle band usually connected by narrow marginal expansion of middle band; apical lunule and middle band not connected; surface shiny or greasy-appearing; *Color:* dorsum and front of head bronze or cupreous, with areas of green and blue; genae blue and green; lateral portions of thorax cupreous, green, and blue; venter green to purplish blue; pronotum bronze or cupreous with depressions green and blue; elytra between markings cupreous to purple-cupreous to bronze to greenish bronze, sometimes quite green when viewed from an oblique angle.

Type locality: Big Salt Marsh, 11 mi. N.E. of Hudson, Stafford Co., Kansas. Holotype male, allotype female, and 15 paratopotypes (11 males, four females), 7 April 1965 (Harold L. Willis) in the Snow Entomological Museum, University of Kansas. Ninety-eight paratopotypes, 9 April 1964, 7 April 1965, 21 June 1965 (Harold L. Willis): ten in the U.S. National Museum; ten in the American Museum of Natural History; 15 in the collection of N. L. Rumpp; five in the collection of G. C. Gaumer; four in the collection of J. Stamatov, Armonk, New York; three each in the collections of R. Freitag, R. C. Graves, R. L. Huber, and J. K. Lawton; two in the collection of J. F. Payne, and the rest in the author's collection. Eight paratopotypes, 23 May 1965 (Paul E. Slabaugh), in the collection of P. E. Slabaugh.

Fourteen paratypes: OKLAHOMA, 2.5 mi. S.W. of Plainview, Woods Co., 3 May 1964, 3 June 1963, 8 June 1965, five specimens in the author's collection; 3 mi. E. of Cherokee, Alfalfa Co., 11 April 1931, 4 June 1963, 7 June 1931, 11 June 1931, 15 June 1935, eight specimens, five in the University of Oklahoma, one in the U.S. National Museum, one in the Museum of Comparative Zoology, Harvard University, and one in the author's collection; NEW MEXICO, 4 mi. E., 1 S. of Arch, Roosevelt Co., 9 June 1965, one specimen in the author's collection.

Distribution: Central Kansas, western Oklahoma, west-central Texas, east-central New Mexico, and possibly west-central New Mexico (Fig. 160).

Diagnosis: Differs from *C. w. willistoni* and *C. w. estancia* in narrower markings, with the humeral lunule and middle band separate or narrowly connected, not broadly confluent; from all other subspecies by the large number of medial setae on the frons and vertex (more than 15, rather than

10 or fewer), the relatively longer labrum (width/length ratio usually less than 2.0, rather than more than 2.0), and the generally reddish brown dorsal color, rather than (usually) dark brown, greenish, or blue. This subspecies shares the very setose head, longer labrum, and reddish dorsal color with *C. w. willistoni* and *C. w. estancia.*

Four out of 24 or 16.7% of specimens of *C. w. hirtifrons* have a labral width/length ratio of 2.0 or greater. Out of 99 specimens representing *C. w. echo*, *C. w. pseudosenilis*, and *C. w. praedicta*, 17 or 17.2% have a labral width/length ratio of less than 2.0; however, these values range from 8.4% for *C. w. echo* to 29.1% for *C. w. praedicta.*

The one specimen from Roosevelt County, New Mexico, has quite wide markings, the apical lunule and middle bands nearly being connected at the margin. The Andrews County, Texas, record is based on a second instar larva. About half the specimens from Oklahoma have slightly wider markings than most Kansas specimens. The record from Beckham County, Oklahoma, is based on Ortenburger and Bird (1933); no specimens have been examined from there. Only about 3% of the Kansas specimens have so much green on the dorsum that they appear green-brown; however, it is a brighter green than occurs in western subspecies. About 4% of the Kansas specimens are a dark brown and might be confused with *C. w. echo*, but the number of head setae easily separates them. All the Oklahoma specimens and the New Mexico specimen are cupreous-brown, with no indication of green. Occasional individuals of *C. w. echo* are reddish brown or reddish green; however, as mentioned, the number of setae on the frons and vertex completely separates the two forms (if the head setae have been rubbed off, one can find what their approximate number was by counting the punctures from which they arose). The exact status of the population at Grants, Valencia County, New Mexico, is not known. No specimens were available for study; however, N. L. Rumpp *(in litt.)* said that they are similar to the Kansas specimens.

I do not know the subspecies of the population in Arizona (Fig. 160) because I have seen no specimens from there. Two specimens reputedly from Orange County, California, that are dark blackish and have fairly wide markings are being called *C. w. echo* for the present. One specimen labelled Alameda County and two from Los Angeles County, California, are typical *C. w. pseudosenilis.*

Wickham (1904a, b) thought that *C. w. echo* arose within the Great Basin, that *C. w. pseudosenilis* has been isolated at Owens Lake, California, since at least early Pleistocene, and that *C. w. willistoni* was separated from the other forms of the species (known to him at that time) by the rising mountains of late Tertiary. Rumpp (1961) postulated that *C. willistoni* arose from an ancestor that lived in northern North America in the warm Cretaceous. As climates cooled during the Tertiary, the ancestral species moved south and became widespread from Colorado to the Pacific coast, gradually assuming the character of *C. willistoni*. He stated that after its formation, *C. willistoni* evolved only slightly, coming through the Miocene "in its present form." The rising mountains of the Cascadian Revolution isolated populations in the Great Basin, Wyoming, and New Mexico. The various subspecies began evolving during the Pliocene or earlier.

Wickham's and Rumpp's theories on the evolution of *C. willistoni* seem quite plausible, although it is hard to imagine that little or no evolution has occurred since the Miocene. The selective forces that acted to produce the different geographic races (matching the color of the substrate seems to be an important one, climatic conditions are another) would seem to be still operating. Wickham and Rumpp did not know of the occurrence of *C. willistoni* in the central United States, and neither mentioned that populations from east of the Rocky Mountains have quite setose heads, while those in the West are sparsely setose (Wickham noted a difference, but only in passing). The closest relatives of *C. willistoni* (it has no extremely close relatives) are *C. senilis* and the *C. tranquebarica* complex, all of which have very setose heads. Thus, I conclude that the primitive condition in *C. willistoni* is a densely setose head, and that the western forms are losing this character. The markings of the ancestral species were probably much like those of *C. w. echo* or *C. w. hirtifrons*, from which expansions or reductions evolved. The primitive color was most likely brownish; populations of *C. w. pseudosenilis* still contain occasional brown or half brown individuals, hinting of its origin from a *C. w. echo*-like ancestor. During the late Tertiary, *C. w. echo* must have been distributed nearly throughout the Great Basin; in fact, it transgressed into eastern Utah and southwestern and south-central Wyoming, leaving relict populations (Fig. 160). During dry interglacials, many populations were no doubt exterminated, leaving large gaps in the range of *C. w. echo*, particularly in eastern Nevada. *C. w. hirtifrons* and *C. w. estancia* probably evolved from a common ancestor (the same one that left populations in Wyoming which became *C. w. willistoni*) that moved south into New Mexico in the Tertiary and then dispersed northeastward through Texas and Oklahoma into Kansas. A population was "trapped" in the Estancia Valley of central New Mexico and became the very widely maculate *C. w. estancia*, while *C. w. hirtifrons* retained a "normal" maculation. The soil in the habitat of the former is tan and sandy, and is usually covered by a white alkaline crust. In the range of *C. w. hirtifrons*, soils are usually red clay or sand, and the climate is moister (especially in the eastern part). Thus, these forms have apparently evolved toward a better match of their substrate.

GENERAL PATTERNS

The seven species discussed exhibit certain general patterns within the central United States. The most striking are the increase in red color (in all but *C. fulgida*) in the region of red soils, and the increase of white maculation in the drier western regions, both of which have been discussed repeatedly above. Another is the distinctness of the populations in the Lincoln, Nebraska, vicinity. Four of the species have more or less distinct forms occurring there: the small, always reddish form of *C. circumpicta*, the black form of *C. fulgida*, the narrowly maculate *C. nevadica lincolniana*, and a form of *C. togata* in which the edges of the white maculation are brownish and indistinct (occasional specimens from northern Kansas show this also). As mentioned earlier, I think this means that these populations survived the last one or two Pleistocene glaciations at this locality, while other populations of their species were driven south or exterminated.

FAUNAL RELATIONSHIPS

The 13 species in this study are divisible into two groups, reflecting their principal distribution and phylogeny: 1) the northern species; these are the more primitive species that are adapted to cooler climates (most active in the spring and fall in the central United States), and that have primarily northern distributions; 2) the southern species; these include the more advanced species that are adapted to warm climates (active in the summer in the central United States), and that have primarily southern distributions. The northern species are *C. duodecimguttata*, *C. fulgida*, *C. hirticollis*, *C. repanda*, *C. tranquebarica*, and *C. willistoni*. The southern species are *C. circumpicta*, *C. cuprascens*, *C. macra*, *C. nevadica*, *C. punctulata*, *C. schauppi*, and *C. togata*. The probable evolutionary relationships of these species were discussed in the section on phylogeny.

SUMMARY

1. Aspects of the bionomics and zoogeography of 13 species of *Cicindela* (Coleoptera: Cicindelidae) living in saline habitats of the central United States (southern Nebraska, western Missouri, Kansas, and Oklahoma) were studied.

2. A review was made of the published works concerning the bionomics of *Cicindela*. By watching beetles in the field and rearing them in the laboratory, new knowledge was obtained on such subjects as oocyte development, gross embryology, length of stadia, pupal development, post-emergence changes of the adult, feeding of larvae and adults, mating behavior, oviposition, and ecological relationships. The larvae of four species were described

for the first time *(C. fulgida, C. nevadica, C. togata,* and *C. willistoni)* and one was redescribed *(C. circumpicta).* The species show a tendency to avoid competition by inhabiting different microhabitats and by being active at different times of the year; however, there is much overlap. Adaptations for living in saline habitats were noted; most are possessed by species not inhabiting such areas, and many of the species in this study are more common in nonsaline habitats.

3. The zoogeography of seven species was studied for their entire ranges *(C. circumpicta, C. cuprascens, C. fulgida, C. macra, C. nevadica, C. togata,* and *C. willistoni*). Geographic variation of morphological characters was studied using generalized discriminant functions. The results were used to help confirm or reject the existence of subspecies. The subspecies *C. circumpicta salinae* and *C. togata fascinans* were rejected. One new subspecies, *C. willistoni hirtifrons,* was described.

4. Using the patterns of geographic variation and evidence from past geological history, hypothetical schemes of evolution and dispersal were proposed. An important selecting pressure acting on all species but *C. fulgida* seems to be increasing the resemblance of the dorsum of the adult to the color of the substrate. In regions having red soil, populations of beetles show a pronounced tendency toward reddish colors. In the drier western parts of their ranges, many species have an increased amount of white on the body, particularly the white elytral markings. This seems to result from the fact that in these areas, saline habitats are more often covered by a crust of white crystalline salts; in moister areas, the salts are more often dissolved and the color of the soil is apparent.

5. It is suggested that the Lincoln, Nebraska, vicinity was a refuge for at least five species during the late Pleistocene glaciations.

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